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The Role of Attention and Perception in the Control of Visually Guided and Memory-Guided Actions

by

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Abstract

I investigated the attentional and perceptional mechanisms involved in the control of visually guided and memory-guided actions in two experiments using event-related potentials (ERPS). In the first dual task experiment, participants performed reciprocal aiming in visually guided and memory-guided modes while simultaneously performing a dichotic listening task from which ERPs were collected. A decrease in mismatch negativity (MMN) component amplitude during visually guided aiming suggests that it requires more automatic attention, and an increase in P300 component latency during memory-guided aiming suggests that it requires more voluntary attention. In the second experiment, ERPs were collected while participants were presented with pictures of tools and, after a delay, either pantomimed how each tool was used (go) or did nothing (no-go). No differences in perception-related N170 amplitude were found between go and no-go trials but limitations of this experiment impede conclusions as to the role of N170 mechanisms in delayed action planning.

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1 General Introduction

The brain can be thought of as a sensorimotor interface that selects information from the environment, processes it, and transforms it into actions. What information is processed and how it is processed, as well as what brain mechanisms subserve these processes, depends on the type of action being performed.

Actions can be divided into immediate actions and delayed actions. Immediate actions are action that are performed on an object you can see, immediately, right in front of you. This type of action is planned using richly detailed online visual information; it is a "visually guided" action. On the other hand, delayed actions are actions initiated on an object when that object is no longer in view. For example, reaching for your coffee cup just after turning away to answer the phone is a delayed action. Depending on the context, delayed actions can be planned using different types of information. If someone has recently acted on an object, similar subsequent delayed actions may be informed by previously created motor plans (Soechting and Flanders, 1989; McVea and Pearson, 2009; McVea et al., 2009). However, if the delayed action has no precedent, multiple lines of evidence suggest that the action is planned using stored perceptual information about the object; it is a "memory-guided action." (The research presented in this paper focuses on this latter type of delayed action.)

Over two experiments, I used ERPs to compare the attentional and perceptual mechanisms involved in controlling visually guided and memory-guided actions. The first experiment, presented in chapter two, examines the attentional mechanisms employed by visually guided and memory guided actions by comparing their effects on the P300, an ERP component associated with voluntary attention, and the mismatch negativity (MMN), an ERP component associated with involuntary attention. The second experiment, presented in chapter 3, examines the perceptual mechanisms employed by memory guided actions by testing if the N170, an ERP component associated with form perception and object identification, is activated by delayed actions.

This chapter will begin with a description of the Goodale and Milner (1992) two stream model of vision, as well as evidence supporting it. The distinction between the brain mechanisms used to control visually guided and memory-guided actions is derived from this model. Next, I will examine evidence suggesting that stored perceptual representations are used to plan memory-guided actions. Following that, I will present evidence that visually guided and memory-guided actions make different demands on attention. Finally, I will explain what ERPs are and how they are used in research. The particular ERP components studied, the P300, MMN, and N170 will be introduced in their respective research chapters. For the purposes of this paper, the term "delayed" action will be used synonymously with “memory-guided” action and the term “immediate” action will be used synonymously with “visually guided” action.

1.1 Two stream action and perception model of vision

Ungerleider and Mishkin (1982) were the first to suggest that the visual system can be separated into two cortical visual streams with separate processing roles. They suggested that the ventral stream, projecting from occipital to temporal cortex, specializes in identifying objects (“what” stream) while the dorsal stream, projecting from occipital to parietal cortex, specializes in locating objects in space (“where” stream).

Based on human neuropsychological work, Goodale and Milner (1992) extended the Ungerleider and Mishkin model. Patients with dorsal stream lesions can describe the relative locations of objects in their visual field perfectly well, although they cannot pick these objects up successfully (Perenin and Vighetto, 1983). More than a deficit in locating objects with their hands, these patients also fail to scale their grip, rotate their hand, and place their fingers properly when attempting to grasp objects. These patients, however, can use information from other sensory modalities, like proprioception or audition to guide their movements. This suggests that their deficit is not in spatial vision, as predicted by Ungerleider’s and Mishkin’s model, nor is it a more general action deficit, but instead it is a deficit in using visual information to control their actions (Goodale, 2008).

Patients with damage isolated to the ventral stream display the converse pattern of deficits and spared abilities. Visual form agnosia patient D.F., the best documented case, cannot identify objects in her visual field or describe their relative locations, but she can pick them up just fine (Goodale et al., 1991). She also cannot “show you what she sees.” In other words, she cannot draw objects in her visual field or demonstrate their properties, like the size or orientation of an object, using her hands. She can still perceive the colour and texture of objects and can recognize objects using these features as well as by tactile features or by the sounds they make when these properties are particularly indicative of the object’s identity.

Patients with a damaged dorsal stream can use vision to perceive objects but cannot use vision to guide their actions on these objects. Patients with a damaged ventral stream can use vision to guide their actions on objects but cannot use vision to perceive objects. This double dissociation motivated Goodale’s and Milner’s (1992) extended model of the visual system.

According to Goodale and Milner (1992), the dorsal and ventral visual streams differ in their relationship to the control of action. The dorsal stream, projecting from occipital to parietal cortex, specializes in transforming visual information into frames of reference used by effectors. The ventral stream, projecting from occipital to temporal cortex, specializes in transforming visual information into representations of the world. In other words, the dorsal stream specializes in vision-for-action and the ventral stream specializes in vision-for-perception.

Vision-for-perception also influences actions, albeit in a more indirect manner, by bringing in knowledge from previous experiences. It identifies dangerous objects and allows them to be avoided, and identifies rewarding objects and allows them to be sought out. For example, consider the task of picking berries to eat. Vision-for-perception distinguishes edible berries from poisonous ones and thus selects appropriate targets for picking. Of course, vision-for-action is involved in transforming this general plan into the series of muscle contractions and extensions that guide the hand to the berries. Similarly, vision-for-perception is critical in selecting where to grasp a tool, because appropriate grasping depends on the tool's identity. Moreover, psychophysical judgments, like indicating the relative size of an object by pressing a button, turning a dial, or opening your hand, typically engage vision-for-perception (Goodale, 2008).

Intuitively, a division of labour in the visual system makes sense because perception and action require visual information to be processed in different ways (Goodale, 2008). Perception is primarily concerned with the identity of objects, regardless of their exact orientation or location. Perception recognizes what different visual scenes have in common, allowing you to bring in all your stored information about similar, previously encountered objects to inform your current situation. Action, on the other hand, is concerned only with the exact, constantly shifting orientation, shape, and location of an object with respect to you, regardless of its identity. Action recognizes how visual scenes are different, allowing you to adapt your actions to the particularities of the situation you are in and perform them successfully.

Further evidence for Goodale's and Milner's (1992) model comes from a study using a modified version of the Ponzo size-contrast illusion. In the regular Ponzo illusion, two identical objects are drawn across a pair of converging lines. The converging lines are like rails on a railway track and the objects drawn across them are parallel to the ties of the track. The illusion is that, even though the objects are identical, the object closer to the converging end of the lines is perceived as longer. In Ganel et al.'s (2008) version, however, instead of using identical pairs of objects they used pairs of objects with different lengths. In many of the trials, the pairs were set up so that their perceived differences and physical differences in length were incongruent. In other words, the object that was perceived as longer was physically shorter and vice versa. When participants were asked to grasp the object that appeared shorter or the object that appeared longer, their choice followed the perceived lengths of the objects, not the real size. However, as they opened their hand to grasp these objects, the aperture between their thumb and forefinger reflected the real, not the perceived size of the objects. The choice of goal object, controlled by vision-for-perception, reflected the perceived size differences and was not influenced by the real size differences, but grip aperture, controlled by vision-for-action, reflected the real size differences and was not influenced by the perceived size differences. Once again, this shows a double dissociation between vision-for-action and vision-for-perception (Ganel et al., 2008).

Some studies have failed to find dissociations between vision-for-perception and vision-for-action using certain visual illusions. For example, Franz et al. (2009) provide evidence that the Müller-Lyer illusion affects both grip aperture when grasping the Müller-Lyer arrows, usually thought to be controlled by vision-for-action, and psychophysical judgments about the arrows' length, usually thought to be controlled by vision-for-perception. However, they admit that these results do not refute the two visual stream model because the Müller-Lyer illusion may result from visual processes that precede the dorsal-ventral split.

Even if this and other similar studies were interpreted as evidence against the perception-action model, they would still fail to undermine research investigating the ways in which immediate and delayed actions are controlled. Goodale's and Milner's (1992) perception action model is important in that many insights about the nature of immediate and delayed actions are derived from research into the perception action model, but the validity of these insights does not depend on the validity of the perception action model.

1.2 Delayed action planning relies on stored perceptual representations

Goodale (2008) argues that delayed action planning differs in its perceptual requirements. Only delayed actions must be planned using vision-for-perception because of the time frames over which vision-for-perception and vision-for-action operate. The relationship of an object with respect to you is constantly changing and so this type of information is only important right now, as an action is performed. As soon as there is the slightest shift in your position or the object's this information becomes obsolete and therefore there is no point in storing it. Also, the amount of detail about the exact absolute parameters of objects in your visual field is too much to store in memory. Perceptual information, on the other hand, may be stored for years and is efficiently adapted for this purpose. Exact dimensions are not computed or stored in perception, but more abstract estimates are. If visual information is not immediately available, Goodale (2008) argues that the vision-for-action stream cannot be used and instead delayed actions must be guided by less accurate stored perceptual representations from the vision-for-perception stream.

However, there is evidence that neurons in the dorsal vision-for-action stream remain active during brief delays between object presentation and action. Murata et al. (1996) identified neurons in the anterior intraparietal sulcus (area AIP) of monkeys whose activity, they argue, is related to visual memory. After the brief visual presentation of an object, these neurons displayed high levels of activity in the dark. Their activity was not related to fixation or to motor preparation. For some of them, their activity was even selective for a certain shape of object, showing significantly higher activity during and after presentation of a ring, for example, than for any other shape of object tested. Similarly, Singhal et al. (2006), using fMRI, discovered that area AIP, located within the dorsal stream, is active during the maintenance phase of a delayed hand action paradigm in humans.

Nevertheless, the behaviour of patients with dorsal or ventral stream lesions suggests that the ventral stream is critical in planning delayed actions. D.F., with the damaged ventral stream, grasps currently visible objects perfectly well but she fails to scale her grip aperture appropriately when she attempts to grasp the object when it is no longer visible (Goodale et al., 1994). I.G., a patient with a damaged dorsal stream, cannot scale her grip properly while attempting to grasp currently visible objects, but her performance improves when she attempts to grasp the object when it is no longer visible (Milner et al., 2001). The patient with the intact vision-for-perception stream performs better after a delay while the patient with the damaged vision-for-perception stream performs worse, suggesting that it is this stream that is critical in guiding delayed actions.

Further evidence comes from Singhal et al.'s (2006) fMRI study of delayed goal-directed hand actions. In their study, fMRI data was recorded while participants reached to or grasped objects in a delayed mode. The action type, either reaching or grasping, was indicated at the beginning of each trial with an auditory cue. Afterwards, a visual target was briefly presented and, after a delay period of 18 seconds, a second auditory cue was delivered. The second auditory cue indicated whether participants should act on the target or do nothing. They found that the lateral occipital cortex (LOC) was reactivated upon initiation of delayed actions even though the visual target was no longer in view. The LOC is a key structure of the ventral visual stream, involved in object recognition and form discrimination (Grill-Spector et al., 2001). It is the same part of the brain that is damaged in D.F. and so its reactivation lends further support to the idea that delayed action planning employs stored perceptual representations.

Behavioural studies also support the relationship between delayed actions and stored perceptual representations. As established by the previously described Ponzo illusion experiment, only vision-for-perception is affected by certain types of illusions. When participants grasp targets in a size contrast illusion, their grip aperture is scaled appropriately to the actual size of the targets. When a delay is introduced between viewing the target and grasping, the grip aperture reflects the perceived size of the target more, suggesting that vision-for-perception has taken over (Westwood and Goodale, 2002).

Finally, further converging evidence comes from a dual task study by Singhal et al. (2007). In this study, participants grasped objects in visually guided and delayed modes while performing a second, shape discrimination task. In the second task, participants listened to object names and said “yes” if the object was round. There was more interference between the shape discrimination task and delayed grasping than visually guided grasping. Singhal et al. (2007) argue that this pattern of data is the result of overlap in information used by the shape discrimination task and delayed grasping. In the shape discrimination task participants retrieved stored perceptual information about the object named and then made a judgment about its shape. The increased interference for delayed grasping suggests that participants also used stored perceptual information about the previously viewed object to plan the action.

1.3 Visually guided and memory-guided action planning relies on voluntary and involuntary attention

Performing actions relies on the selection process of attention. Grasping an object, for example, requires selecting one target from many in a complex visual scene and then selective processing to extract information necessary to perform the grasp (like the size of the object, its position, and so on). Attention may be directed to an object in two ways, either because its physical salience captures attention (involuntary attention), or because it is consciously selected (voluntary attention). Involuntary attention is driven by objects themselves, because of an inhomogeneous feature or features that make them 'pop-out' from other objects. On the other hand, voluntary attention is consciously focused on stimuli irrespective of saliency or 'pop-out.'

When voluntary attention is not a factor, activity in a number of sensory brain areas is dominated by salient stimuli (Näätänen, 1990; Kayser and Petkov, 2005; Moore, 2006). Stimuli compete for representation in a mutually suppressive way where more salient stimuli win out by suppressing their competition more strongly than they themselves are suppressed (Kastner and Ungerleider, 2000). This automatic focusing of attention can feed forward to higher brain areas via direct or indirect connections. For example in the visual system, a cortical column in area V1 connects directly to a column in area V2 and also connects indirectly to the V2 column through the pulvinar nucleus of the thalamus (LaBerge, 1998). The same type of direct and indirect thalamic pathways are used in the auditory system (LaBerge, 1995). Voluntary attention is also mediated through thalamocortical circuits. Sites of voluntary attentional control in the prefrontal and parietal cortex are thought to modulate activity in sensory areas through thalamic relay neurons projecting to those areas (LaBerge, 1998).

Depending on the context in which visually guided actions are performed, they may or may not make use of voluntary attention. In an experiment by Deubel and Schneider (2006), participants had to move their finger to reach a target at the same time they determined the shape of a briefly presented (80 ms) discrimination target. The reach target and discrimination target could be presented at the same or different locations, and participants were either shown the location of the reach target a few hundred milliseconds before they initiated their movement, or at the same time they initiated their movement. When the reach target and discrimination target were presented at the same place, discrimination performance was almost perfect, but when they were presented at different locations discrimination performance deteriorated. This suggests that visually guided reaching is using voluntary attention, and impeding its deployment to the discrimination target. However, this interference only occurred when the reach target and discrimination target were presented at the same time. When participants were given time to preview the reach target before initiating their movement, discrimination performance returned to near perfect levels. This shows that visually guided actions can be performed without voluntary attention deployment if participants are given adequate time to prepare their movement.

Similarly, the role of involuntary attention in visually guided action planning seems to depend on timing. This evidence comes from an experiment by Wood et al. (2011). In their experiment, participants rapidly reached towards an array of multiple targets where the final target was cued only after the reach was initiated. One target in the array was higher salience than the others and thus more likely to draw involuntary attention. When participants were instructed to initiate their reach at the same time the array was presented, their reach trajectories were biased more towards salient targets. However, if participants were given time to preview the array before initiating their movement, their reach trajectory reflected a spatial average of the positions of the targets and was not more strongly influenced by the salient target. This shows that visually guided actions are influenced more by involuntary attention when participants do not have time to prepare their movement.

Memory-guided actions rely on voluntary attention. Ostendorf et al. (2004) tested the speed with which participants could discriminate a target during the memory phase of a memory-guided saccade task. While participants fixated a central cross, a peripheral cue was briefly presented (0.5 s). Six seconds later, participants would be asked to saccade to the remembered cue position. At some point during the delay interval, a letter was presented and participants had to indicate what letter it was as fast as they could. They found that discrimination was slowed by the memory-guided saccade task, but interference was strongest when the letter was presented at the same place as the saccade cue and when the memory-guided saccade was more accurate. This spatially selective interference illustrates the voluntary attentional requirements of memory-guided actions.

As you can see from the previous few sections, delayed action planning emphasizes different cognitive resources than immediate action planning. The evidence supporting this position comes from neuropsychological, fMRI and behavioural studies. ERP studies have only just begun to investigate these differences. As ERPs are the focus of my research, they will be introduced next.

1.4 Event-related potential components represent stages of processing

Electroencephalography (EEG) is the recording of brain activity at the scalp. An ERP is a subset of EEG activity: it is brain activity recorded at the scalp that is associated with a particular sensory, cognitive, or motor event (Luck, 2005a). The brain, of course, is constantly processing innumerable events simultaneously and so the ERP associated with any one event must be a subset of all of the EEG activity recorded. This, unfortunately, makes ERPs difficult to visualize in recordings of a single event. A motor ERP associated with initiating a reaching movement, for example, will be obscured in raw EEG by activity associated with the countless other operations simultaneously being performed by the brain, not to mention sources of environmental electrical noise, changes in skin conductance, eye movements and other artifacts that contaminate brain activity recordings. In order to isolate activity specifically associated with the event in question, the typical procedure is to repeat the event hundreds of times and average together the EEG activity surrounding each event. Averaging takes out activity that is not associated with the event and leaves you with what is. After averaging, the resulting sequence of positive and negative voltage changes is the ERP waveform.

ERP waveforms elicited by an event are very similar for an individual subject across multiple recording sessions (low within-subject variability) but there are often large differences between ERP waveforms from different subjects (high between-subject variability) (Luck, 2005a). The cause of between subject variability is thought to be individual differences in the cortical folding pattern (Luck, 2005a). The folding pattern affects the orientation of the cortical generators of ERPs, which in turn affects the morphology of the waveform recorded at each electrode. This means that the amplitude and latency of particular peaks in the ERP waveform can differ substantially between subjects and this jitter leads to grand average waveforms that are more attenuated than their individual subject counterparts (Luck, 2005a).

Some questions of interest can be answered using the whole ERP waveform by itself, without further decomposition into discrete ERP components. For example, you can determine if an event is processed differently in two conditions by comparing the ERP waveforms elicited by the event in each condition. A significant difference in amplitude or topography is likely due to a difference in processing. You can find out when processing differences first start by looking at the latency of the earliest difference. This type of analysis can tell you *if* and *when* conditions differ, but it cannot tell you *how* they differ.

Examining ERP components can tell you *how* conditions differ (Luck, 2005b). Each component is associated with certain cognitive processes, based on the contexts that elicit the component and the types of manipulations that have been found to affect it. The extent a component differs between conditions allows you to infer the extent their associated cognitive processes differ. Even the simple activation of a component is informative in that it may reveal an unexpected cognitive process that is elicited by an event.

Consider the lateralized readiness potential (LRP) as an example. LRP activation indicates response preparation. In a typical go/no-go experiment, where one type of stimulus indicates that a participant should make a response, and another type of stimulus indicates that a response should be withheld, an LRP will be elicited by the go stimulus but not by the no-go stimulus. Miller and Hackley (1992) used the LRP to determine if response preparation would be elicited by no-go stimuli when the cue to respond or not was a difficult to discriminate secondary feature of a stimulus. In their modified go/no-go experiment, the shape of the stimulus indicated what type of response to make, while the size of the stimulus indicated whether or not to make a response. Miller and Hackley (1992) found that, in this scenario, no-go stimuli briefly elicited an LRP even when no response was made. By examining a particular component, the LRP, Miller and Hackley (1992) were able to identify that a particular process, response preparation, was elicited unexpectedly by no-go stimuli.

Sometimes, when researchers are only interested in a particular feature of an event, they attempt to isolate the components associated with just this feature by subtracting one ERP from another (Luck, 2005b). For example, if a researcher was interested in the components associated with processing the size of a visual stimulus, that researcher could collect ERPs elicited by large stimuli and small stimuli separately, and then subtract these ERPs from each other. The resulting difference wave would contain only those components associated with processing stimulus size.

The difficulty in examining components is that, unfortunately, there is no generally agreed upon definition of an ERP component, although several attempts have been made. Otten and Rugg (2005) point out that definitions usually go one of two ways. One anatomical extreme defines a component as a part of the ERP originating from a unique anatomical source. The other physiological extreme defines a component as a part of the ERP associated with a particular functional process. Modern definitions of a component, like Otten's and Rugg's, tend to blend these two approaches. Otten's and Rugg's (2005) definition, which I will use, is:

> "A part of the [ERP] waveform with a circumscribed scalp distribution (alluding to the underlying neural configuration) and a circumscribed relationship to experimental variables (alluding to the cognitive function served by the activity of this configuration)."

It is important to emphasize why Otten and Rugg define a component partially in terms of its scalp distribution, and not its source. Every scalp distribution could be the result of an infinite number of source configurations (Slotnick, 2005). This is called the inverse problem, and it is one of the reasons why it is difficult for researchers to agree on the source(s) of a component. Because of this difficulty, Otten and Rugg instead define components in terms of their scalp distribution.

In the following chapters, I will present experiments that use ERP components to investigate the attentional and perceptional mechanisms underlying visually guided and memory-guided actions. ERP components that reflect attentional and perceptual mechanisms will be described and the effect that visually guided and memory-guided actions have on them will be observed. Any interaction between these actions and these components suggests an overlap in the mechanisms underlying each. This is important in that it can both elucidate the way these actions are controlled and further clarify the processes these components reflect.

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2 Neural markers of automatic and controlled attention during immediate and delayed action[1]

2.1 Introduction

A significant problem in cognitive psychology is to understand the nature of the relationship between the human attention and action systems. Traditionally these aspects of behaviour have been studied separately, or have been considered to lie at opposite ends of the stimulus-response continuum. However, it is likely that there is substantial overlap between their underlying processes (Hommel, Ridderinkhof, and Theeuwes, 2002), although the nature of their interactions may depend upon the types of action being performed (Singhal, Culham, Chinellato and Goodale, 2007). In order to further examine the neural bases of some of these relationships between attention and action, I designed a dual-task experiment that recorded event-related potentials (ERPs) during an auditory attention task while participants performed a concurrent reciprocal aiming task under conditions of varied visual feedback.

A major theme in attention research has been to understand the nature of bottom-up automatic (involuntary) processes compared to top-down control

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(voluntary) mechanisms, where automatic processes can operate outside of the executive focus of attention, and controlled processes rely on executive functions such as working memory. Moreover, voluntary controlled attention can be deployed to various spatial locations and objects and is considered slow and sustained. On the other hand, automatic attention is captured by salient (exogenous) stimuli and is considered fast and transient (Norman and Shallice, 1986; LaBerge, 1995; Serences and Yantis, 2006). This is particularly important when considering attentional processes in action since motor control processes can also be highly automatic (e.g., breathing) or under cognitive control (e.g., using a tool for the first time).   In the case of selective attention, one requirement is that information from the environment is briefly retained in order to determine whether it is task relevant. This involves controlled processing and likely relies on an intimate relationship between attention and memory processes subserved by an overlap in the neural mechanisms underlying each process. Functional imaging studies of visual selective attention and memory have supported this position (LaBar et al., 1999; Cabeza et al., 2003), some arguing that working memory is vital for attentional control (Kastner and Ungerleider, 2000; deFockert et al., 2001). This has implications for models of attentional control during action, particularly delayed actions that presumably also require the memory processes of encoding, storage and retrieval. That is, if delayed actions require more memory processing about the spatial location and object properties of the target compared with immediate actions, they may also rely on controlled aspects of attention more than immediate actions. Moreover, there may be effects that depend on the differential requirements of spatial versus object-based attention processes subserving action.

2.1.1 Neural mechanisms of immediate (visually guided) actions versus delayed (memory-guided) actions

There is a large body of converging evidence suggesting that actions under the immediate control of vision rely on separate neural mechanisms from actions that require memory for their guidance. For instance, it has been argued that immediate actions rely on fast acting automatic (involuntary) mechanisms in the posterior parietal cortex of the dorsal visual stream (Goodale, Milner, Jakobson, and Carey, 1991; Jeannerod, Arbib, Rizzolatti, and Sakata, 1995; Binkofski et al., 1998; Astafiev et al., 2003; Culham et al., 2003). However, in the case of actions that are delayed and thus not under direct visual control, emerging evidence points to reliance on higher-order perceptual and memory mechanisms in the inferior temporal cortex of the ventral visual stream (Goodale, Westwood, and Milner, 2004).

Compelling neuropsychological evidence has shown that visual form agnosia patient D.F., who has damage to her ventral visual stream, performs very well immediately reaching out and grasping a visible object, but cannot scale her grip aperture properly when attempting to grasp an object that was removed from view (delayed) 2 s earlier (Goodale et al., 1994). This result shows that D.F. had no memory of the size and shape of the goal object, perhaps because her damaged ventral stream prevented encoding of the critical perceptual information about the object (Goodale et al., 1994), and strongly indicates that the brain mediates delayed action differently than immediate visually guided action. This position is further supported by work with the optic ataxia patient, I.G., who has bilateral damage in the dorsal visual stream (posterior parietal cortex), but an intact ventral stream. Even though I.G. is unable to scale her grip when she attempts to grasp visible objects, her grip scaling improves significantly when she pantomimes a grasping movement to an object viewed 5 s earlier (Milner et al., 2001). Taken together, these two studies provide strong evidence that delayed actions rely on stored perceptual information that is initially processed by mechanisms in the ventral visual stream, and raise the possibility that the dorsal stream may not even be necessary for delayed actions (Goodale et al., 2004).

Additional evidence for this position comes from work showing that delayed movements are more sensitive to perceptual illusions than are visually guided movements (Westwood, Chapman, and Roy, 2000; Westwood, Heath, and Roy, 2000; Westwood, McEachern, and Roy, 2001). For example, Hu and Goodale (2000) presented participants with target blocks adjacent to companion blocks of differing size. The presence of the companion blocks induced an illusion in which a target accompanied by a smaller companion block was perceived to be larger than a target of the same size accompanied by a larger companion. When the participants were asked to reach out and grasp the target block with full vision their grip aperture was scaled appropriately to the real size of the target and was not affected by the size-contrast illusion. However, most importantly, when a 5-s delay was imposed between target viewing and action initiation participants opened their hand wider when the target was accompanied by a smaller companion block than when it was accompanied by a larger one. This suggests that the scaling of the delayed actions employed information about the earlier perception of the target that led to the size contrast illusion effect in the first place (Westwood and Goodale, 2003). Furthermore, research examining the nature of delayed pointing compared to immediate pointing with visual feedback shows that the pattern of location errors associated with delayed pointing indicate that egocentric distances may be underestimated due to the nature of the stored sensory representations of the target underlying memory-guided action (Heath and Binstead, 2007).

One interpretation of the pattern of results of these studies is that that the brain goes into an “offline” perceptually driven mode as soon as vision of the target is removed, and that “online” visuomotor mechanisms are only engaged when the target remains visible during the programming of the movement.

Moreover, these studies strongly suggest that delayed actions depend on memory processes associated with perceptual encoding, storage and retrieval in order to calibrate the movement, perhaps engaging perception-based cognitive mechanisms that mediate other tasks that rely more explicitly on perceptual 'imagery' and working memory. Additional support for the position of the perception based nature of delayed action comes from an fMRI study that showed clear-cut reactivation of a well know perceptual brain region in the ventral stream; the lateral occipital cortex (LOC), when neurologically intact subjects grasped remembered objects after an 18 s delay (Singhal et al., 2006). On the other hand, Kroliczak et al., (2007) showed that pantomimed grasping did not activate LOC more than real grasping, which is curious considering the fact that patient D.F. demonstrates pantomimed grasping deficits as well as delayed action deficits. However, one difference between Kroliczak et al. (2007) and Singhal et al. (2006) is that the former did not insert an extended delay period between stimulus presentation and the initiation of action. It is important to note that other studies have shown that when a different measure of perception (an adjustment task) is used, the perceptual reports are not more sensitive to pictorial illusions (typically, the Ebbinghaus illusion) than visually guided grasping (Franz, Gegenfurtner, Bulthoff, and Fahle, 2000; Franz, 2001, 2003; Franz, Bulthoff, and Fahle, 2003).

2.1.2 Dual-task evidence

In dual-task studies, participants concurrently perform two qualitatively different tasks that are designated as primary and secondary. The key assumption underlying this approach is that an increase in difficulty or priority of the primary task will lead to a decrease in the amount of available resources for secondary task performance (Pashler, 1994). Furthermore, in dual-task studies when interference exists between two task factors, it is assumed that those factors tap resources that are similar in nature to each other and presumably engage similar neural processes and structures (Gopher and Donchin, 1986). Using this logic, Singhal et al. (2007) had participants make immediate or delayed grasps while performing a secondary auditory shape identification task (experiment 1) where participants had to make verbal judgments about whether a presented word described a round object or not. In experiment 2, the second task was an object-based paired-associate task, where participants had to verbally declare a target word when prompted by the cue. Both auditory tasks involved memory and likely taxed working memory operations. The authors in that study also speculated that these auditory tasks involved mental imagery processes. The results showed that delayed grasping interfered more with performance on the auditory task compared with immediate grasping, and moreover, the auditory task interfered more with delayed grasping performance compared to immediate grasping. This reciprocal interference suggests that delayed actions share more perception-based information processing with imagery/memory tasks compared to visually guided actions. A second conclusion is that since there was more dual-task interference between delayed action and the secondary task; delayed action likely shares more resources with a voluntary attention system that controls the allocation of resources and mediates performance between two tasks in two sensory modalities (vision & audition) (Singhal et al., 2007). In another dual-task study, Liu, Healy and Enns (2003) employed two action tasks as follows: (1) a direct action task, which required participants to point directly to a target position, and (2) an indirect action task, where participants had to consciously indicate a target location by pressing a corresponding key that was in a different location than the target. In the dual-task conditions, each of these tasks was paired with a visual search task. The main results showed that indirect pointing performance was disrupted more by visual search compared to direct pointing. Based on dual-task logic, the authors suggest that their results are due to unique attentional mechanisms subserving each type of action. Moreover, they argue that the direct action task likely involves automatic, dorsal stream processes and the indirect action likely reflects more ventral stream processes, due to the cognitive control requirements of that task (Liu et al. 2003). Taken together, these two studies support the idea that the dual-task paradigm can be an effective method to investigate the nature of cognition underlying action.

2.1.3 ERP markers of attention

One well established ERP marker of attentional processes under voluntary control is the P300 waveform. Extensive literature supports the idea that the P300 wave has multimodal generators (see Kok, 2001) and peaks once a task relevant stimulus has been evaluated. It is typically observed when attention is paid to a stimulus train which has both frequent and infrequent (oddball) trials. It has been shown that the peak latency of the P300 increases if the categorization of a target stimulus becomes more difficult suggesting it is also involved in low-level perception (Kutas, McCarthy and Donchin, 1977; Coles, Smid, Scheffers and Otten, 1995). Furthermore, the P300 is considered to reflect early perceptual processes more than response related processes because cognitive interference tasks such as the STROOP paradigm lead to longer reaction times and response-related ERP latencies compared to P300 latency changes (Kok, 2001). In the case of P300 amplitude, there is some agreement that it reflects the intensity of processing (Donchin et al., 1986; Donchin, Kramer, and Wickens, 1986; Kok, 1990; Polich and Kok, 1995) as well as perceptual-central resources (Donchin, et al., 1986; Donchin, Kramer, and Wickens, 1986; Kramer & Spinks, 1991) within a multiple capacity framework (Wickens, 1984). In dual-task studies, P300 amplitude has been shown to be sensitive to cognitive load involving perception and working memory (Isreal, Chesney, Wickens, and

Donchin, 1980; Isreal, Wickens, Chesney, and Donchin, 1980; Wickens, Kramer, Vanasse, and Donchin, 1983; Sirevaag, Kramer, Coles, and Donchin, 1989; Singhal and Fowler, 2004; 2005).

Much work has also examined the neural generators of the P300 component. In a recent study co-registering ERP and fMRI data, the brain networks underlying the visual P300 (oddball P3b) were localized to both parietal cortex and inferior temporal cortex (Bledowski et al., 2004). The auditory P300 has been localized to a large network including the superior temporal gyrus (STG), anterior cingulate, supplementary motor regions, and the tempo-parietal junction (TPJ) (Mulert et al., 2004). There is also neuropsychological evidence showing that auditory P300 latency is longer in patients with TPJ lesions (Alonso et al., 1996). Finally, it has been long argued that the multimodal nature of P300 may be due to significant frontal lobe contribution (Johnson, 1993).

Another ERP that is known to reflect human attentional processes is the mismatch negativity (MMN). During dichotic listening MMN is elicited by a deviant stimulus in a stream of standard stimuli and is observed best as a difference wave made by subtracting the standards from the deviants in the unattended ear of the dichotic task. Thus, this difference waveform reflects the processing of the deviant stimuli occurring outside of the awareness of the direct focus of attention. Näätänen (1990; 1992) argues that MMN reflects an automatic (involuntary), modality specific feature detection system that is not sensitive to voluntary attentional manipulations. This position has been supported by studies that have shown MMN is insensitive to concurrent visual task demands (Alho, Woods, Algazi, and Näätänen, 1992; Otten, Alain, and Picton, 2000; Singhal, Doerfling and Fowler, 2002). However, the argument that the MMN is purely automatic and encapsulated from other processes has been disputed on the basis of evidence that it can be attenuated under conditions of highly focused attention within the auditory modality (Woldorff, Hackley, and Hillyard, 1991; Woldorff, Hillyard, Gallen, Hampson, amd Bloom, 1998). There are also two studies that have shown that auditory MMN can be attenuated by concurrent visual stimuli when the auditory task involves single channel stimulus presentation (Kramer, Trejo and Humphrey, 1995) as well as novel environmental sounds (Yucel, Petty, McCarthy and Belger, 2005). The neural generators underlying the MMN have been identified as significantly involving bilateral areas in the supratemporal auditory cortex as well as the frontal lobes (Giard et al., 1990; 1995). More recent fMRI work has shown that in addition to auditory cortex involvement, the parietal cortex is largely recruited during change detection processes underlying MMN generation, perhaps as part of an automatic attention switching mechanism (Molholm, et al., 2005).

2.1.4 Primary research questions in the current study

There is considerable evidence that delayed actions rely on different circuitry than immediate actions; yet, to date, no work has utilized electrophysiological techniques in human participants to further explore this despite the excellent temporal resolution afforded by this technique. Based on the foregoing review two main research questions have emerged for the purposes of the present dual-task experiment. Since a major proportion of the work investigating the neural bases of delayed actions have strongly suggested that they involve the use of perceptual mechanisms and the literature shows that changes in P300 amplitude likely reflects perceptual-central mechanisms and changes in P300 latency likely reflect lower level perceptual mechanisms, I (1) asked whether delayed actions would influence the latency and amplitude of P300 more than immediate actions. Since it has been argued that immediate actions are automatic in nature (compared to delayed actions) I (2) asked whether they are more closely linked to the attentional processes reflected by the MMN.

To address these questions I designed a cross-modal dual-task experiment with a primary reciprocal aiming task modified from Fitts (1954) with both immediate and delayed conditions and a secondary auditory attention task with both attended and unattended trial types. The ERPs were collected from the auditory task, and I hypothesized that in the dual-task, the two primary task conditions would differentially affect the morphology of the P300 and MMN components (Gopher and Donchin, 1986).

2.2 Methods

2.2.1 Participants

Eighteen right-handed adult paid volunteers (12 women) with a mean age of 21.4 years (SD = 1.9, range 19-25 years) were recruited for this experiment. All reported normal hearing and normal or corrected-to-normal vision. Ethics approval was obtained from the University of Alberta Research Ethics Board, and the participants gave their informed consent.

2.2.2 Reciprocal Aiming Task

The primary task was a joystick-controlled reciprocal aiming task modified from Fitts' classic tapping paradigm (Fitts, 1954). Participants were positioned approximately one meter away from a wide-screen, 48.26 cm monitor displaying two rectangular targets. Using their dominant (right) hand, participants moved an on-screen crosshair cursor back and forth between the targets with a thumb and finger-operated resistive joystick (CH Products, Vista, CA, US). The relative position of the joystick corresponded directly to the position of the on-screen cursor. There were two conditions in this task: 1) a visually guided (VIS) condition where both targets remained completely visible throughout the entire condition and 2) a memory-guided (MEM) condition where each target disappeared just prior to; and for the entire duration of the participants' movement towards it. For example, in the case of a leftward movement in the memory-guided condition the left target disappeared from view when the previous movement to the right target was completed, but prior to the initiation of leftward movement (i.e. prior to turnaround). I make the assumption that this procedure forced participants to plan their movement to each target without vision (Goodale et al., 2004).

Task difficulty varied with target width. The index of difficulty (ID) was calculated in the following manner: ID = $\mathrm{Log}_2\,(2A/W)$ bits, where A was the distance between the centers of the targets and W was the width of each target in the plane of movement (Fitts, 1954). The amplitude, held constant at 200 mm, and the combination of three different target widths (40, 20, and 10 mm) resulted in IDs of 3.32, 4.32, and 5.32, respectively. The visual angle between the outer edges of the targets was 13.75 degrees for ID 3.32, 12.61 degrees for ID 4.32, and 12.03 degrees for ID 5.32.

The dependent measures were the following: (1) movement time (MT), and (2) target accuracy as a percentage (successes/total trials x 100%).

2.2.3 Dichotic Listening Task

The auditory task consisted of 10 blocks of 100 non-overlapping tones (50 ms duration, 10 ms ramp, 67 dB SPL) presented through stereophonic earphones (KOSS 4 A). The frequent standards (1000 Hz, 80% probability) and the infrequent deviants (1500 Hz, 20% probability) were presented randomly as a rectangular distribution with a mean inter-tone interval (offset to onset) of 700 ms and a range of 500-900 ms to either the left or right ear for a total of 50 tones/ear/block. The participants were required to pay attention to a designated ear and report the infrequent deviants with a button press with their non-dominant (left) hand. Reaction time (RT), accuracy as a percentage, and EEG activity were recorded from this task. Errors included misses and false alarms, but the latter were very rare, and the two categories were pooled for the purposes of analysis.

2.2.4 Recording and Quantification of EEG

Silver-silver chloride (Ag-AgCl) electrodes were attached at Fz, Cz, and Pz positions (see appendix A), referenced to linked ears, and grounded to the forehead with an impedance of 5kOhm or less. Electro-oculographic (EOG) electrodes were attached to the outer canthus and supra-orbital region of the right eye. The signals were amplified (GRASS Neurodata Acquisition System 12B) with a band-pass of 0.1-30 Hz (-6dB, 9dB/octave rolloff). The EEG and EOG were digitized every 5 ms for a 1500 ms epoch, which included a 100 ms pre-stimulus baseline that was used for statistical measurement. The EEG data were corrected for saturation and eye movements (Gratton, Coles, and Donchin, 1983). Initially, all the ERP data were viewed by eye, and the peaks for each waveform of interest were identified for each of the participants. Then, custom peak picking software measured the peak amplitude and latency of the P300 and MMN. The P300 was defined as the most positive peak in the range 270-600 ms (post-stimulus) range in the attended deviant tones' waveforms. The MMN was defined as the most negative peak in the 100-200 ms (post-stimulus) range in difference waves derived as follows: unattended deviants - unattended standards.

2.2.5 Design and procedure

A repeated measures design was used with a total of 13 conditions. EEG activity from the auditory task was collected in seven of those conditions: one control and six experimental. In the EEG control condition, the auditory task was performed alone (LISTEN), with no visual stimuli other than a white fixation cross. The six experimental dual-task conditions paired the auditory task with the six aiming task conditions: visually guided at each ID (DUAL VIS 3.32, DUAL VIS 4.32, and DUAL VIS 5.32), and memory-guided at each ID (DUAL MEM 3.32, DUAL MEM 4.32, and DUAL MEM 5.32. The other six conditions were the visual control conditions where the aiming task was performed alone: visually guided at each ID (AIM VIS 3.32, AIM VIS 4.32, and AIM VIS 5.32), and memory-guided at each ID (AIM MEM 3.32, AIM MEM 4.32, and AIM MEM 5.32). The experiment was performed in two separate sessions on two separate days: one session for the seven EEG conditions, and one for the six visual alone conditions. The order of the sessions and the order of the conditions within a session were counterbalanced using a Latin square design. To achieve stable performance, prior to the experiment the participants were trained on both the auditory and visual tasks. Training typically lasted 10-20 minutes. They were instructed to be 100% accurate, and reached the performance criteria when they performed at 85% accuracy on both tasks. The visual task was designated as primary and the auditory task was designated as secondary. That is, I instructed the participants to adopt an attentional strategy where they performed the primary task at the expense of the secondary task (Gopher & Donchin, 1986). The data were analyzed using one-way, two-way, or three-way repeated measures ANOVAs with Greenhouse-Geisser epsilon corrections, followed by contrasts corrected with the modified Bonferroni procedure (Keppel, 1991).

2.3 Results

2.3.1 Behavioural measures

Table 2-1 shows the average movement times (MT) and percent accuracy for the primary aiming task in the alone and dual-task conditions. Table 2-1 also contains the mean correct RT and accuracy data for the secondary auditory task in the alone and dual-task conditions. See appendix B for plots of means.

2.3.2 Primary aiming task: movement time

As expected from Fitts (1954), a 2 (alone/dual) x 2 (VIS/MEM) x 3 (ID) ANOVA on the MT data revealed a main effect of ID [F (2, 34) = 100.02, E = 0.599, P < 0.00001]. Planned contrasts confirmed significant differences between each ID level (3.32 vs. 4.32 P <0 .00001; 4.32 vs. 5.32, P < 0.000001). There was also a main effect of condition (VIS/MEM) [F (1, 17) = 39.44, P < 0.00001] where the MEM conditions were slower than the VIS conditions. MT did not differ between aiming alone and aiming in the dual-task.

2.3.3 Primary aiming task: accuracy

A 2 (alone/dual) x 2 (VIS/MEM) x 3 (ID) ANOVA on the primary aiming accuracy revealed an interaction between condition (VIS/MEM) and ID [F (2, 34) = 31.4, E = 0.747, P < 0.000001]. Planned comparisons revealed that this interaction was due to differences in accuracy between the VIS and MEM conditions at the two most difficult IDs: 4.32 ($P < 0.004$) and 5.32 ($P < 0.00001$). There was also main effect of ID level [F (2, 34) = 190.34, E = 0.834, $P < 0.00001$]. Planned comparisons revealed that accuracy decreased as a function of ID level ($P < 0.00001$). Finally there was a main effect of condition (VIS/MEM) [F (1,17) = 111.78, $P < 0.00001$) revealing that accuracy was lower in the MEM aiming conditions compared with the VIS conditions.

2.3.4 Auditory task: RT and accuracy

A one-way repeated measures ANOVA on RT revealed an effect of performing both tasks concurrently (cost of concurrence) [F (6, 102) = 30.80, E = 0.750, $P < 0.00001$]. The slowing in RT was observed from the LISTEN control condition to all of the DUAL conditions; (DUAL VIS 3.32, $P < 0.000001$; DUAL VIS 4.32, $P < 0.000001$; DUAL VIS 5.32, $P < 0.0000001$; DUAL MEM 3.32, $P < 0.0000001$; DUAL MEM 4.32, $P < 0.0000001$; DUAL MEM 5.32, $P < 0.0000001$)). A 2 (VIS/MEM) x 3 (ID) ANOVA on RT revealed a main effect of condition (VIS/MEM) [F (1, 17) = 13.44, $P < 0.002$], and a main effect of ID [F (2, 34) = 16.21, E=0.910, $P < 0.00001$]. A similar pattern was observed in the auditory task accuracy data. A one-way repeated measures ANOVA revealed a cost of concurrence [F (6, 102) = 9.27, E = 0.50, $P < 0.00006$]. The decrease in accuracy was observed from the LISTEN control condition to the DUAL VIS 4.32 condition ($P < 0.04$) as well as all three DUAL MEM conditions ($P < 0.01$). A 2 (VIS/MEM) x 3 (ID) ANOVA revealed a main effect of condition (VIS/MEM) [F (1, 17) = 11.58, P < 0.003], and a main effect of ID [F (2, 34) = 10.46, E=0.713, P < 0.001]. Planned comparisons revealed that the decrease in accuracy was from the easiest ID (3.32) to the most difficult (5.32).

2.3.5 ERP measures

Figure 2-1 shows the grand average waveforms elicited by the attended target (deviant) tones during dichotic listening at electrodes where P300 was maximal (Cz and Pz). Figure 2-2 shows the grand average waveforms elicited by the unattended deviant and standard tones during dichotic listening at Fz and Cz. Figure 2-3 shows the mismatch negativity (MMN) difference waves at Fz and Cz. Table 2-2 contains the mean amplitudes and latencies for P300 and MMN. See appendix B for plots of means.

2.3.6 P300

A one-way repeated measures ANOVA on P300 amplitude revealed a cost of concurrence at the Pz electrode from the LISTEN control condition to the dual-task VIS conditions [F (3, 51) = 5.10, E = 0.725, P < 0.009; contrast; LISTEN vs. DUAL VIS 3.32 P < 0.005]. There were no differences between the DUAL VIS conditions. A one-way repeated measures ANOVA on P300 amplitude revealed a cost of concurrence at the Pz electrode from the LISTEN control condition to the dual-task MEM conditions [F (3, 51) = 3.95, E = 0.674, P < 0.002; contrast; LISTEN vs. DUAL MEM 4.32 P < 0.003]. There were no differences between the DUAL MEM conditions. In the case of P300 latency a one-way repeated measures ANOVA revealed a cost of concurrence at Pz [F (3, 51) = 6.00, E = 0.787, P < 0.003]. The slowing was observed from the LISTEN control condition to all three of the DUAL MEM conditions (DUAL MEM 3.32, P < 0.04; DUAL MEM 4.32, P < 0.04; DUAL MEM 5.32, P < 0.04). There were no significant latency differences between the LISTEN condition and the DUAL VIS conditions. A 2 (VIS/MEM) x 3 (ID) ANOVA on P300 latency revealed a main effect of condition (VIS/MEM) [F (1, 17) = 5.00, P < 0.03] where there was greater slowing in the MEM conditions compared with the VIS conditions. There was also a strong trend (P < 0.057) for ID level on P300 latency at Pz in the DUAL MEM conditions. This trend was due to longer P300 latency in the 4.32 and 5.32 ID conditions compared with that in the 3.32 ID conditions.

2.3.7 MMN

A one-way repeated measures ANOVA on MNN amplitude revealed a cost of concurrence at Fz [F (3, 51) = 3.56, E = 0.916, P < 0.02]. The attenuation was observed from the LISTEN control condition to the DUAL VIS 3.32 condition (P < 0.04) and the LISTEN control condition to the DUAL VIS 4.32 condition (P < 0.02). There was no difference between the control condition and the DUAL VIS 5.32

condition. There was also no cost of concurrence in the DUAL-MEM conditions. This pattern of data was the same at Cz [F (3, 51) = 6.43, E = 0.863, P < 0.001]. The attenuation was observed from the LISTEN control condition to the DUAL VIS 3.32 condition (P < 0.003) and from the LISTEN control condition to the DUAL VIS 4.32 condition (P < 0.005). There was no difference between the control condition and the DUAL VIS 5.32 condition. There was also no cost of concurrence in the DUAL-MEM conditions.

2.4 Discussion

The primary aim of the current study was to examine the nature of the respective attentional requirements in both immediate (visually guided) and delayed (memory-guided) actions. I combined primary reciprocal aiming under two viewing conditions with secondary dichotic listening in a dual-task paradigm. I analyzed behavioural measures in both tasks as well as ERP data collected from the secondary auditory attention task. Our specific research questions were (1) whether delayed actions would influence the latency and amplitude of P300 more than immediate actions and (2) whether immediate actions would influence the amplitude and latency of the MMN. Our main results showed that P300 latency was longer in the dual-task memory condition compared to the immediate condition, suggesting that more perception based processing is required for memory guided action. On the other hand, MMN amplitude was reduced in the dual-task immediate condition, but not in the memory condition. This suggests that more automatic attention resources were required for immediate visually guided task performance compared to the delayed memory–guided action task.

In the visual task I observed a typical increase in MT as ID level increased. This is consistent with many studies (e.g., Fitts, 1954; Fitts and Peterson, 1964; Keele, 1986) and is considered to reflect the increase in motor planning demands for ballistic and corrective movements as difficulty increases (Jeannerod, 1994). In our study I added a modified condition where the onscreen target disappeared prior to and for the duration of the movement toward it. In this case, the linear relationship between MT and ID level remained consistent with the VIS condition, but overall the MTs were slower. This is consistent with delayed action tasks such as reaching and grasping where MT typically increases relative to immediate actions, and it has been argued that the slowing reflects the offline perceptual processing requirements (Westwood and Goodale, 2003; Singhal et al, 2007). What is particularly interesting about our MT data is that there was no effect of the introduction of the auditory task on either the VIS or MEM aiming conditions. One explanation is that the nature of the reciprocal actions in our task was highly rhythmic (Schaal et al., 2004) and thus was not susceptible to the cognitive interference of the auditory task. This point also suggests that our task is unique compared to many of the tasks employed in the perception-action literature, which typically involve discrete pointing and grasping actions. Finally, I argue against the possibility that there may have been effects related to the fact that the visual-task alone conditions were collected on a separate day from all the dual-task conditions. It seems more reasonable to assume that performing the primary task alone on a separate day would increase performance such that any dual-task effects would appear larger.

As expected, the behavioural results from the auditory task show that the introduction of both VIS and MEM conditions of the visual reciprocal aiming task slowed auditory RT and increased errors. This finding is consistent with many dual-task studies (see Pashler, 1984). It is of interest to note that since the VIS aiming condition has target presentation for longer periods of time, there is possibly more error monitoring and correction going on. Based on our results, I argue that these processes are likely highly automatic in nature.

2.4.1 Effects on P300

In the case of the P300 I observed a clear cut decrease in amplitude with the introduction of the primary task compared to the auditory control condition alone. This effect was equivalent between the VIS and MEM aiming tasks, and there was no effect of ID level in either aiming condition. This pattern of data is highly expected and consistent with many studies that have examined the attenuation of auditory P300 amplitude under cognitive load perhaps due to limits in working memory capacity (Wickens et al., 1983; Sirevaag et al., 1989; Kok, 2001; Singhal and Fowler, 2004; 2005). Perhaps the most interesting finding in this study concerns P300 latency. Here, I observed a cost of concurrence in P300 latency with the introduction of the primary MEM aiming task, but not the VIS aiming task. Furthermore, there was a small effect on P300 latency when the ID level increased in the MEM aiming task. These results are interesting when considered within the framework of the delayed action literature. For instance, it has been argued that, compared with immediate visually guided actions, delayed actions rely more on perceptual brain mechanisms (Goodale, 2008), and P300 latency changes are also considered to reflect perceptual operations involved in stimulus identification and categorization (Kok 2001) within the temporal cortex (Alonso et al., 1996; Mulert et al., 2004). Thus, the greater effect of MEM aiming compared to VIS aiming on P300 latency may be due to greater interference from common mechanisms used in the MEM aiming and auditory tasks. Moreover, I suggest that the overlap in attentional mechanisms between the two tasks may reflect controlled processes particularly connected to object-related attention (Duncan, 1984). That is, since the P300 is elicited by the rare “type-selection” process of the auditory task, it seems reasonable to assume that the overlap with the MEM action task is particularly related to object-related attention more than spatial attention. However, our study cannot rule out the possibility that the spatial nature of the reciprocal aiming task in the MEM conditions (but not the VIS conditions) increased P300 latency since that waveform was elicited by stimuli on the attended side of space. This possibility would rely on the assumption that the P300 elicited by a spatial dichotic listening task is substantially different in nature from the P300 elicited by an auditory oddball task that is delivered in stereo. Along this line, our latency analyses on the unattended deviant stimuli (top of Fig. 2) did not reveal a difference in the P300 latency range, suggesting that spatial processes alone are not responsible for the interference effects, but rather the effect may be due to a combination of focused object-based and spatial attention in audition. Also, the planning required by the VIS aiming condition may be more automatic and involuntary and thus can be performed with less overall dual-task interference (Passingham, 1996) on P300 latency. Thus, I argue that the MEM aiming condition may rely on more ventral stream processes (compared with the VIS condition), and the additional interference in P300 latency is due to interference with perceptual mechanisms in the temporal cortex that underlie both this ERP component and delayed action.

The P300 results in this study are supported by the behavioural data from the auditory task. Particularly, auditory RT was slowed more by the introduction of the MEM task compared to the introduction of the VIS task. This suggests a greater overlap in processing resources between auditory selective attention and the MEM condition of the primary aiming task. Of key interest was that I observed an effect of primary task ID level on auditory RT suggesting that the difficulty manipulation in both VIS and MEM aiming conditions taxed auditory selective attention processing. Thus, in contrast to the visual task, the auditory task appeared to be less automatic and encapsulated; and was sensitive to both the VIS/MEM manipulation as well as the ID level manipulation. One possibility for the one-way interference effect of the action task on the auditory task but not the auditory task on the action task is that the aiming task was primary and the auditory task was secondary and the participants maintained their focus on the aiming task at the expense of the secondary task. I think this explanation is unlikely because the same auditory attention task has been used in several other dual-task studies that employed demanding primary visual tasks. For example, simulated flying (Singhal et al., 2002), Sternberg memory scanning (Singhal and Fowler, 2004; 2005), and Posner attention switching (Meehan et al., 2005; Ramirez et al., 2005). In all of those studies, the auditory attention task influenced the visual task to some degree. Thus, I argue here that the aiming task did not show any interference because the reciprocal and rhythmic nature of the actions is highly automatic (Schaal, Sternad, Osu and Kawato, 2004). See Armstrong and Singhal (2011) for additional kinematic data that supports this position.

2.4.2 Effects on MMN

The second ERP component of interest in this study was the MMN. Here I observed a cost of concurrence in MMN amplitude with the introduction of the VIS aiming task, but not for the MEM aiming task. Thus, only the visually guided task had an effect, and the effect was only in the 3.32 and 4.32 ID conditions. This is an interesting finding for three reasons. First, in line with our second hypothesis, I did not observe an attenuation of MMN with the introduction of the MEM aiming task. One possibility is that the memory-guided action task primarily relies on neural mechanisms that are not reflected in the MMN. That is, less automatic, more perceptual-cognitive operations. Thus, in our aiming task, the lowest two VIS conditions may only require low level motor planning and execution mechanisms. Winstein et al., (1997) used PET scanning to show that full vision reciprocal aiming employs a cortical network of pre-motor, SMA, and parietal regions. Since MMN also relies on parietal cortex (Giard et al., 1990), our MMN effect may be due to interference between operations within parietal cortex. In the case of VIS aiming, parietal regions are involved in the online planning of the movements, and in the case of the auditory attention task, the parietal cortex is involved in automatic attentional switching toward a deviant sound (Molholm et al., 2005). Second, in the VIS conditions, the MMN was only attenuated in the two least difficult conditions (IDs of 3.32 and 4.32, but not 5.32). This is interesting and I speculate that it may be due to the fact that at the highest ID level more perceptual-cognitive resources are required in the aiming task, perhaps reducing the overall load on an automatic and encapsulated system. Third, our MMN results challenge Näätänen’s (1990; 1992) idea that MMN is modality specific since I have shown its sensitivity to the load imposed by a cross-modal dual-task. Our results are in line with those of Yucel et al. (2005) who showed that a primary continuous visuomotor tracking task can attenuate the MMN generated by novel environmental sounds that subjects were instructed to ignore. Taken together with our results, it appears that MMN reflects an automatic change detection process that is resource-limited in nature.

2.4.3 Conclusion

In this study, I observed an incomplete reciprocity between an auditory attention task and a visuomotor task with two conditions (immediate and delayed action). That is, the visual tasks interfered with auditory task behavior, but the auditory task did not interfere with visuomotor task behaviour. Moreover, the auditory P300 showed more sensitivity to the delayed action task suggesting that there is more competition for resources within the temporal cortex between voluntary attention processes and memory-guided action. On the other hand, the MMN showed more sensitivity to the immediate action task suggesting that there is more competition for resources within the parietal cortex between automatic attention processes and visually guided action.

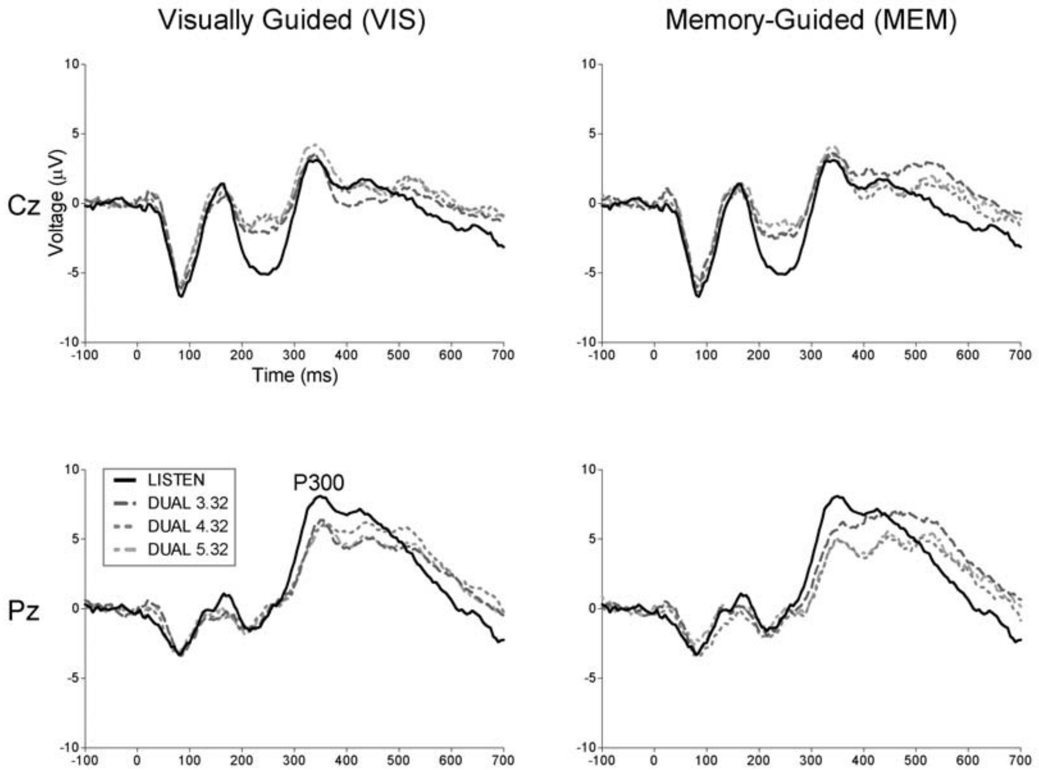

Figure 2-1 Attended deviant waveforms
Grand average waveform from auditory attended deviants at Cz and Pz for the dichotic listening control (LISTEN), and dual task with Fitts aiming in both the VIS and MEM conditions at ID 3.32 (DUAL 3.32), ID 4.32 (DUAL 4.32), and ID 5.32 (DUAL 5.32).

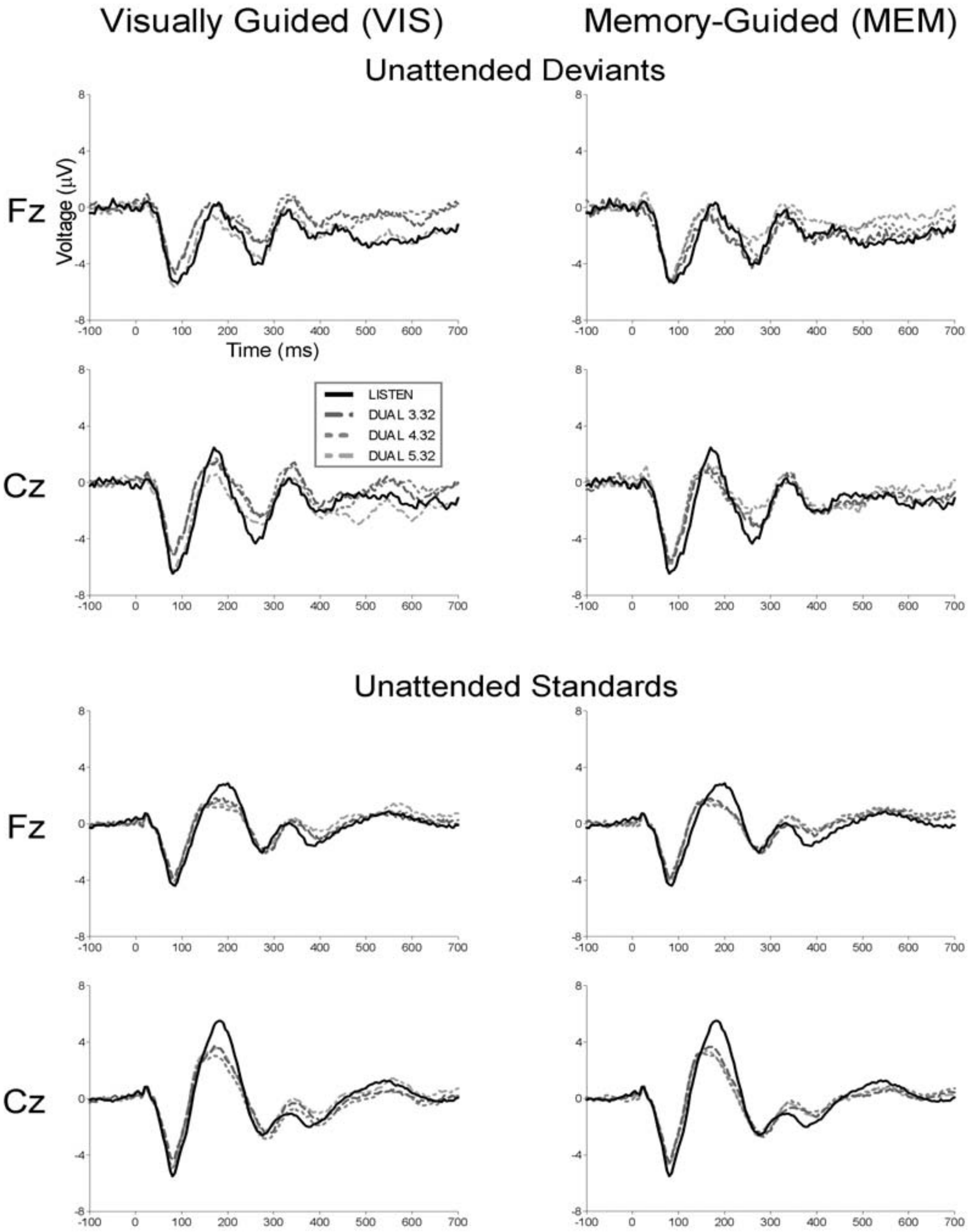

Figure 2-2 Unattended deviant and unattended standard waveforms
Grand average waveforms from auditory unattended deviants and unattended standards at Fz and Cz for the dichotic listening control (LISTEN), and dual task with Fitts aiming in both the VIS and MEM conditions at ID 3.32 (DUAL 3.32), ID 4.32 (DUAL 4.32), and ID 5.32 (DUAL 5.32).

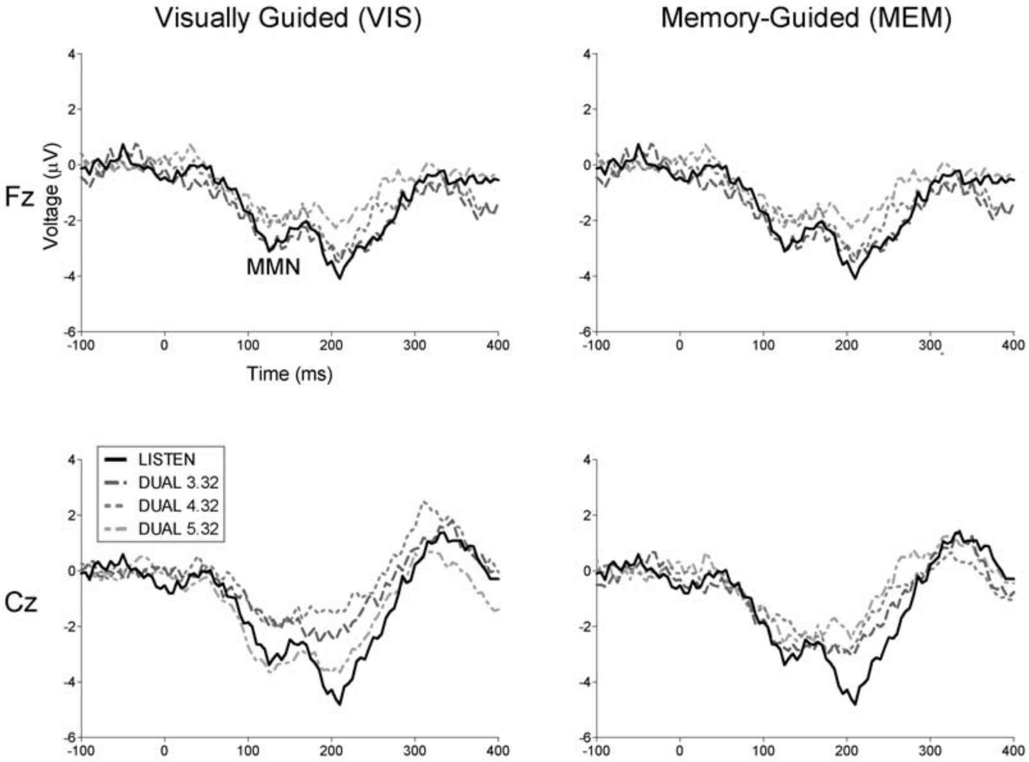

Figure 2-3 MMN waveforms
Grand average auditory mismatch negativity (MMN) waveforms at Fz and Cz for the dichotic listening control (LISTEN), and dual task with Fitts aiming in both the VIS and MEM conditions at ID 3.32 (DUAL 3.32), ID 4.32 (DUAL 4.32), and ID 5.32 (DUAL 5.32).

Table 2-1 Mean performance (and standard error) for aiming and dichotic listening tasks

	Auditory Alone	Vision			Memory		
		ID 3.32	ID 4.32	ID 5.32	ID 3.32	ID 4.32	ID 5.32
Aiming alone							
Movement time (ms)	-	730 (60)	1001 (66)	1400 (92)	1183 (70)	1451 (88)	1716 (115)
Accuracy (%)	-	96.5 (0.6)	91.2 (1.7)	78 (2.2)	92.1 (1.3)	77.2 (2.0)	48.8 (2.7)
Aiming dual							
Movement time (ms)	-	670 (32)	900 (33)	1321 (66)	1140 (41)	1411 (61)	1680 (83)
Accuracy (%)	-	96.9 (0.6)	91.3 (1.3)	79.1 (1.9)	93.1 (1.1)	76.5 (2.5)	50.3 (2.7)
Dichotic listening							
Reaction time (ms)	373 (12)	437 (11)	445 (10)	470 (10)	458 (8)	465 (10)	489 (10)
Accuracy (%)	96.5 (0.6)	94.3 (1.1)	93.5 (1.2)	94.1 (1.2)	91.4 (1.4)	90.6 (1.3)	87.1 (2.2)

ID index of difficulty

Table 2-2 Mean amplitude (in microvolts ± SE) and latency (in ms ± SE) for P300 and MMN

Component, elect.	Auditory Alone	Vision			Memory		
		ID 3.32	ID 4.32	ID 5.32	ID 3.32	ID 4.32	ID 5.32
Amplitude							
P300, Cz	5.7 (1.5)	4.8 (0.7)	4.2 (0.7)	5.3 (1.1)	5.4 (1.1)	4.7 (0.9)	5.1 (0.9)
P300, Pz	10.9 (1.3)	8.3 (0.9)	8.3 (1.0)	8.2 (1.1)	9.6 (1.2)	8.6 (0.9)	8.3 (0.8)
MMN, Fz	-5.4 (0.5)	-4.6 (0.4)	-3.9 (0.6)	-5.2 (0.5)	-5.0 (0.4)	-4.7 (0.4)	-5.0 (0.4)
MMN, Cz	-6.2 (0.6)	-4.6 (0.4)	-3.8 (0.5)	-5.7 (0.5)	-5.3 (0.5)	-5.0 (0.4)	-5.3 (0.5)
Latency							
P300, Cz	396 (15)	401 (25)	409 (24)	403 (22)	438 (21)	420 (22)	429 (26)
P300, Pz	404 (15)	393 (22)	432 (18)	429 (21)	450 (20)	471 (20)	476 (20)
MMN, Fz	171 (13)	165 (16)	156 (17)	180 (12)	176 (13)	173 (13)	172 (12)
MMN, Cz	181 (8)	162 (14)	147 (13)	173 (10)	156 (12)	159 (10)	168 (12)

ID index of difficulty

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3 Perceptual mechanisms underlying delayed pantomimed actions

3.1 Introduction

A major issue in action research is to elucidate the perceptual mechanisms used to plan actions. However, the particular perceptual mechanisms required depends on the type of action to be performed. In this study, I investigated delayed pantomimed actions.

Pantomimes are actions demonstrating the use of an object in the absence of the object itself. For example, one could pantomime swinging a hammer by curling the fingers of one hand and swinging the forearm in the air. In terms of gesture classification, pantomimes share some properties with both transitive and intransitive gestures. Like transitive gestures pantomimes involve an object, albeit an implied object, and like intransitive gestures pantomimes are symbolic in that they symbolize the object and action being mimed. Neuropsychological evidence, however, suggests that pantomimes are distinct from both transitive and intransitive gestures. Bartolo et al. (2003) describe patient V.L., who can perform both transitive and intransitive gestures normally but frequently makes errors when asked to pantomime. This suggests that pantomimes are a unique action type with their own underlying neural mechanisms.

The pantomimes investigated in this study are delayed. There is abundant evidence that when there is a delay between viewing an object and acting on it action planning relies on stored perceptual representations. For example, delayed grasping is sensitive to perceptual illusions (Franz, Hesse, and Kollath, 2009; Hu and Goodale, 2000; Westwood, Chapman, and Roy, 2000; Westwood and Goodale, 2003; Westwood, McEachern, and Roy, 2001). When participants are presented with an object whose perceived dimensions do not accurately reflect its real dimensions because of an illusion, and are then asked to grasp this object after it is removed from view, their grip aperture reflects the inaccurate perceived dimensions of the object.

Along the same lines, in dual task studies there is greater interference between tasks that involve visual imagery or memory and tasks that involve delayed actions compared to immediate visually guided actions (Armstrong and Singhal, 2011; Singhal et al., 2007). This suggests that delayed action planning has more resources in common with visual imagery and memory than immediate action planning does.

Further evidence comes from neuropsychological studies. Visual form agnosia patient D.F. cannot identify objects in her visual field and she also fails to scale her grip aperture properly when attempting to grasp an object that was just removed from view even though she has no problem grasping objects that are immediately visible (Goodale, Jakobson, and Keillor, 1994). On the other hand, optic ataxia patient I.G. can use vision to perceive objects, and she also scales her grip aperture better when grasping objects after a delay than when grasping currently visible objects (Milner et al., 2001). For both patients visual perceptual performance and delayed action planning performance are associated. This strongly supports a connection between delayed action planning and perception.

The ventral visual stream, projecting from occipital to temporal cortex, has been implicated in the perceptual processing critical for delayed action planning. Part of the ventral visual stream, the lateral occipital cortex (LOC), is bilaterally lesioned in patient D.F. (James et al., 2003). The LOC is involved in visual object recognition and form discrimination so D.F.'s impaired visual perception and impaired delayed action planning are likely a result of this LOC damage (Grill-Spector, Kourtzi, and Kanwisher, 2001).

However, Murata et al. (1996) identified another brain area that they suggested may play a role in delayed action planning. In monkeys, they found that neurons in the anterior intraparietal sulcus display high levels of activity in the dark after the visual presentation of objects. Some of these neurons were even selective for certain object shapes. Nevertheless, the role of parietal cortex in delayed action planning is dubious considering I.G.'s spared delayed action planning abilities in spite of bilateral parietal cortex damage.

The most direct evidence of the ventral stream's involvement in delayed action planning comes from Singhal et al.'s (2006) functional magnetic resonance imaging (fMRI) study of a delayed action task with go and no-go trials. In their study, fMRI data were recorded while participants acted on objects in a delayed mode. A visual target was briefly presented and, following a delay period, an auditory cue was delivered. This cue indicated whether participants should act on the target (go) or do nothing (no-go). They found that the LOC was reactivated upon initiation of delayed actions, even though the visual target was no longer in view, and this reactivation was significantly greater in go than in no-go trials. This establishes an fMRI correlate of the perceptual processes involved in delayed action planning: LOC activation.

An event-related potential (ERP) correlate of the perceptual processes involved in delayed action planning has yet to be firmly established. In contrast to fMRI, which follows the blood-oxygen-level-dependent (BOLD) contrast, ERPs are based on electrophysiological recordings that may reflect different neural mechanisms. An ERP correlate could be valuable because it has much greater temporal resolution than the BOLD response. It could make the study of the temporal dynamics of delayed action planning possible.

Based on the preceding discussion, the ERP correlate of the perceptual processes involved in delayed action planning would likely meet the following three criteria: (1) Changes in its morphology or topography should be linked to visual perceptual processing, (2) Changes in its morphology or topography should be tied to memory, and (3) it should have a generator located in the ventral visual stream. Based on the following evidence, the N170 is a likely candidate.

Although the N170 was first described in the context of face perception, responding differently to faces compared to other object categories, it has since been found to reflect more general visual perceptual processes (Bentin et al., 1996). The N170 responds differently to several different object categories. It is left lateralized for words, right lateralized for faces and bilateral for most other objects (Rossion et al., 2003). It is also larger in amplitude for objects than grayscale noise (Sreenivasan et al., 2007). The way the N170's morphology and topography varies depending on object category demonstrates its link to visual perceptual processing.

The N170 is also modulated by the memory requirements of a task. At encoding, Bankó and Vidnyánszky (2010) found that N170 amplitude in response to a stimulus varies based on how long the stimulus will need to be retained in memory. In a study by Sreenivasan et al. (2007), face and house memory items in a delayed recognition task were separated from their test items by several grayscale visual noise probes. The visual noise probes were used to assess working memory processes throughout the delay interval. As expected, the face memory items evoked a larger N170 than house memory items, but surprisingly, this N170 advantage carried over to the visual noise probes that followed presentation of faces. Grayscale noise probes presented up to four and a half seconds (the longest delay tested) after face memory items elicited a larger N170 than the same probes presented after house memory items. This shows that N170 morphology can reflect processing of stimuli that are no longer visible, which is critical because the targets of delayed actions are not visible when delayed actions are planned.

Bankó and Vidnyánszky's (2010) study also shows that the N170 can be reactivated by memory. The N170 elicited by the probes shows reactivation of the memory item. This point is crucial because memory retrieval reactivates some of the sensory brain regions active during encoding (Wheeler, Petersen, and Buckner, 2000). Given all the evidence that delayed actions require retrieval of perceptual memories I can infer that delayed action planning likely relies on sensory reactivation. Therefore, the N170 is a likely candidate because it reflects the initial processing of a visual stimulus and can also be reactivated by memory processes.

Furthermore, Cruikshank et al. (2012) have recently studied visually guided and memory-guided actions using the N170. In their study, participants reached for visual targets on a touch sensitive monitor as soon as a beep cue was delivered. In the memory guided condition, the target was removed from view at the same time the beep was delivered, forcing participants to plan their reach based on a perceptual memory of the target's location. In the visually guided condition, the target was not removed from view until participants had initiated their reach and moved from the starting position, allowing them to plan their movement using immediately available visual information. The N170 elicited after the beep, prior to reach initiation, was larger in the delayed condition than the visually guided condition, potentially implicating the perceptual mechanisms reflected by the N170 in delayed action planning. However, it is important to notice that in the memory-guided condition the cue to initiate the reach was delivered at the same time as the removal of the target. Several studies suggest that when visual information changes concurrently with the delivery of the cue to act the action is planned using different types of information than when participants have a few hundred milliseconds to adapt to the change in visual information before acting (Deubel and Schneider, 2003; Wood et al., 2011).

Finally, one study has even localized a generator of the N170 to the ventral visual stream. Rossion et al. (2003) provide evidence that one generator of the N170 is in the LOC, the same area that Singhal et al. (2006) found to be reactivated during delayed action planning.

Based on this evidence, the N170 component meets all three criteria. Changes in the morphology and topography of the N170 have been linked to (1) visual perceptual processing and (2) memory, and (3) the N170 has a generator in the ventral visual stream. Therefore, I can ask if N170 activity reflects perceptual processes recruited by delayed action planning. In order to answer this question, in this study I recorded ERPs while participants performed a delayed pantomime action paradigm with go and no-go trials. Participants were briefly presented with a picture of a tool and, after a delay, either pantomimed how they would use the tool (go), or did nothing (no-go).

I chose to use tools because they are complicated stimuli which elicit larger N170s, because the affordances for action they provide naturally draw visual attention, and because of their reliance on perception in order to be used properly (Handy et al., 2003). You must know what kind of tool you are looking at to match it with the appropriate hand posture for its use. Tool use is also tied to memory. In Creem and Proffitt's (2002) study, for example, participants generally picked up tools in a manner appropriate for their use, unless their memory was taxed. When participants had to grasp tools while recalling target words from a paired-associated list, they still grasped the tools successfully but did so in a manner inappropriate for their use.

Pantomimed actions also have a foundation in the two visual streams literature. D.F., the patient with impaired delayed grasping, also performs poorly when asked to pantomime grasping beside an object (Goodale et al., 1991; 1994). On the other hand, I.G., the patient with impaired immediate grasping, performs better when pantomiming (Milner et al., 2001). This suggests involvement of the ventral visual stream in performing pantomimed actions.

However, an fMRI study of real and pantomimed grasping failed to find a relationship between LOC activation and pantomimed grasping (Kroliczak et al., 2007). Furthermore, an ERP study comparing memories of real and pantomimed tool actions only found differences over frontal and frontocentral cortex (Senkfor, 2007). The present study is an opportunity to test if delayed pantomimed tool actions rely on the ventral visual stream.

In summary, the main goal of the present study is to test whether N170 activity reflects processes recruited by delayed pantomimed action planning. A corresponding goal is to test if delayed pantomimed actions rely on perceptual ventral stream processes. Following Singhal et al.'s (2006) study that found greater LOC activation for go than no-go trials on a delayed action task, I reasoned that if N170 activity is correlated with the processes required for delayed pantomimed action planning there should be stronger N170 activation for go than no-go trials. Stronger N170 activation would also be evidence that delayed pantomimed actions rely on perceptual processes.

3.2 Methods

3.2.1 Participants

21 right-handed participants (11 female) between 20 and 30 years of age, (mean = 24.1 years, SD = 3.3 years) reporting normal hearing and normal or corrected-to-normal vision were recruited for this experiment. They were paid

CAD$15/hour for their participation. Ethics approval was obtained from the University of Alberta Research Ethics Board and participants gave their informed consent.

Data from 1 participant was excluded from analysis because more than half of her ERPs contained significant artifacts after ocular artifact correction.

3.2.2 Procedure

Participants performed a delayed pantomime action task with go and no-go trials (figure 1). Participants began each trial depressing a response box button with their right hand and fixating a cross at the center of a computer monitor directly in front of them. After 1 second, the fixation cross was briefly replaced by a picture of a tool for 0.5 s, which was then followed by a 2.5 s to 3 s delay. Finally, one of two types of beeps was delivered. For one beep type, called the go beep, delivered 50% of the time, participants released the response box button, pantomimed using the tool with his or her right hand, and then returned to holding down the response box button (go). For the other beep type, called the no-go beep, delivered the other 50% of the time, participants did nothing (no-go). Trials were divided into 8 blocks of 27 trials for a total of 216 trials, 108 go and 108 no-go.

3.2.3 Stimuli

3 examples each of 12 different types of tools were shown for a total of 36 tool pictures. Each tool picture was presented at the center of the monitor in a different orientation for 3 go trials and 3 no-go trials. Each picture was a maximum of 14 cm high and 14 cm wide. Therefore, the maximum visual angle was 11.42 degrees between the outer edges of each image. Tools were selected so that they could be grasped and used with only one hand.

The two types of beeps were a pure beep and a pink noise beep, matched in length, (50 ms), pitch (1000 Hz), and loudness (67 dB). At the beginning of each block, one type of beep was designated as the go beep and the other was designated as the no-go beep. These instructions were counter-balanced; for half the blocks pink noise beeps indicated go trials and for the other half pure beeps indicated go trials.

3.2.4 Behavioural Analysis

Reaction time for go trials and percent accuracy for go and no-go trials was measured. Reaction time was defined as the difference between the time of beep onset and the time the response box button was released. On go trials, errors of omission occurred when participants failed to release the button, and on no-go trials, errors of commission occurred when participants released the button.

3.2.5 Electroencephalographic Recording and Analysis

Electroencephalographic (EEG) signals were recorded using a 256 channel Electrical Geodesics (Eugene, OR) sensor net. Voltages at the scalp were recorded at 250 Hz, and then filtered with a 0.1 Hz high-pass filter and a 30 Hz low-pass filter. ERPs were segmented around tool onset and beep onset, starting 200 ms before and continuing to 400 ms after stimulus onset. Bad channels were replaced with interpolated data based on surrounding channels, and ocular artifacts like blinks and large eye movements were corrected (Gratton, Coles, and Donchin, 1983). Trials including behavioural errors were omitted. Finally, trials were averaged together, grand average re-referenced, and baseline corrected.

Peak picking software measured the N170 following go and no-go beep onset. N170 was defined as the most negative peak in the 140 to 220 ms post-stimulus window.

3.2.6 Statistical Analysis

To test for differences between conditions, I used repeated measures ANOVAs with Greenhouse Geisser epsilon corrections, followed by contrasts corrected with the modified Bonferroni procedure (Keppel, 1991). One analysis of amplitude was conducted restricted to International 10-20 System occipito-temporal electrode sites where the N170 is maximal (see appendix A) (Rossion and Jacques, 2008; Rousselet, Husk, Bennett, and Sekuler, 2008). Condition (go/no-go) and electrode site (P5/P6/PO7/PO8/P7/P8/P9/P10) were within-group factors.

3.3 Results

3.3.1 Behavioural Measures

Average reaction time was 654.7 ms (SE = 40.1 ms). Accuracy was very high for both go (mean = 99.8%, SE = 0.1) and no-go trials (mean = 98.6%, SE = 0.6), and although participants were more accurate for go trials, a paired t-test revealed that this difference was not significant ($P > 0.05$).

3.3.2 ERP Measures

Figure 2 shows grand average waveforms elicited by go and no-go beeps and tool presentation at electrodes where N170 is maximal, and table 1 contains the mean N170 amplitude for the go and no-go conditions at these electrodes.

3.3.3 N170

A two-way repeated measures ANOVA with condition (go/no-go) and electrode site (P5/P6/PO7/PO8/P7/P8/P9/P10) as within group factors revealed differences in N170 amplitude between electrodes [$F(7,140) = 4.281$, $P < 0.0001$], but no differences in amplitude between the N170 elicited by go beeps and the N170 elicited by no-go beeps [F (1, 20) = 4.198, P > 0.05].

3.4 Discussion

The primary goal of this study was to determine if the N170 component is a marker for perceptual processes used in planning delayed actions. I predicted that if the N170 is a marker, it would have a larger amplitude for go than no-go trials, but I did not find any N170 amplitude differences.

These N170 results do not correspond to the results from Singhal et al.'s (2006) fMRI go/no-go delayed action study, which found differences between go and no-go trials at the LOC, despite the fact that the N170 has a generator in the LOC. There are a few possible explanations. One is that the N170 may occur too early to catch go/no-go differences in perceptual processing. As mentioned previously, fMRI has poor temporal resolution and it is impossible to tell exactly when the differences in LOC activation begin based on fMRI data. Differences may start after the N170 component is already complete. Assuming the differences do occur during the N170 time window, other possible explanations are that the changes in neural activity that led to increased blood flow to the LOC were separated from the N170 generator or were not oriented or grouped appropriately to affect N170 amplitude at the scalp.

These results also do not correspond to Cruikshank et al.'s (2012) study, which found increased N170 amplitude for memory-guided actions compared to visually guided actions. There are a few important differences between Cruikshank's study and my own, however, which may explain our different results. First of all, I used different types of actions: Cruikshank used reaching while I used tool pantomiming. While neuropsychological evidence suggests that pantomimes rely on ventral stream processes, Kroliczak et al. (2007) were unable to find ventral stream activation in an fMRI study of pantomimed action performance in intact individuals. I may have failed to find N170 activation because pantomimed actions simply may not employ perceptual processing, even when the pantomime is delayed. Second of all, Cruikshank used much shorter delays than I did. In Cruikshank's study, the cue to initiate reaching and the removal of vision of the reach target occurred at the same time, while in my study the cue to initiate pantomiming occurred several seconds after the picture of the tool had been removed. The way a delayed action is planned might change depending on the length of the delay and N170 mechanisms might only be involved at short delays. Finally, ERPs elicited by delayed actions were compared to different control ERPs in Cruikshank's and my studies. In Cruikshank's study delayed action ERPs were compared to immediate action ERPs, while in this study delayed action ERPs were compared to no action (or inhibiting delayed action) ERPs. It could be that the N170 does reflect processes that play a role in delayed pantomimed action planning but these processes are not inhibited in no-go trials so no difference in N170 amplitude is observed. In this view, if delayed pantomimes had been compared to visually guided pantomimes a difference in N170 amplitude should be found.

As you can see, a lack of differences between go and no-go N170 amplitude does not support the idea that N170 activity reflects perceptual processing used in delayed action planning, but it certainly does not rule it out. It is possible that the N170 is epiphenomenal. For example, Sreenivasan, Katz, and Jha (2007) found that working memory maintenance of visual stimuli leads to top-down modulation of N170s elicited by grayscale visual noise probes. It is possible that the beeps in this experiment function similarly to these grayscale visual noise probes, indexing memory of the previously presented visual stimulus. In this view go and no-go N170 activation is the same because memory of the tool is the same at the time of the beep.

Another possibility is that, in order to plan their pantomimes, participants may have relied on long-term memories of tools as opposed to memories of the recent images presented. Actions based on long-term memories of objects do not rely on the same perceptual processes as other types of delayed actions. For example, D.F. can make reasonable line drawings of objects based on long-term memories (Servos, Goodale, and Humphrey, 1993). If long-term memories were used, then the perceptual processes required for most other types of delayed actions would not need to be invoked and the question of whether the N170 reflects perceptual processing critical for planning delayed actions that cannot rely on long-term memories, like delayed grasping or reaching, remains open.

In summary, in this study I found no differences in N170 amplitude between go and no-go trials. This might be because the N170 does not reflect the processing of stored perceptual representations key for delayed action planning. It might be because pantomimed actions do not rely on ventral stream processes, even when they are delayed. It might be because of the long delay used between tool presentation and action initiation. It might be because the N170 does reflect perceptual processing key for delayed action planning but it occurs too early to be inhibited in no-go trials and thus no difference in N170 amplitude is seen between go and no-go trials. Or, it might be because planning delayed pantomimed actions does not invoke the perceptual processing used by most other types of delayed actions and instead relies on long-term memories of objects. Deciding between these alternatives requires further research.

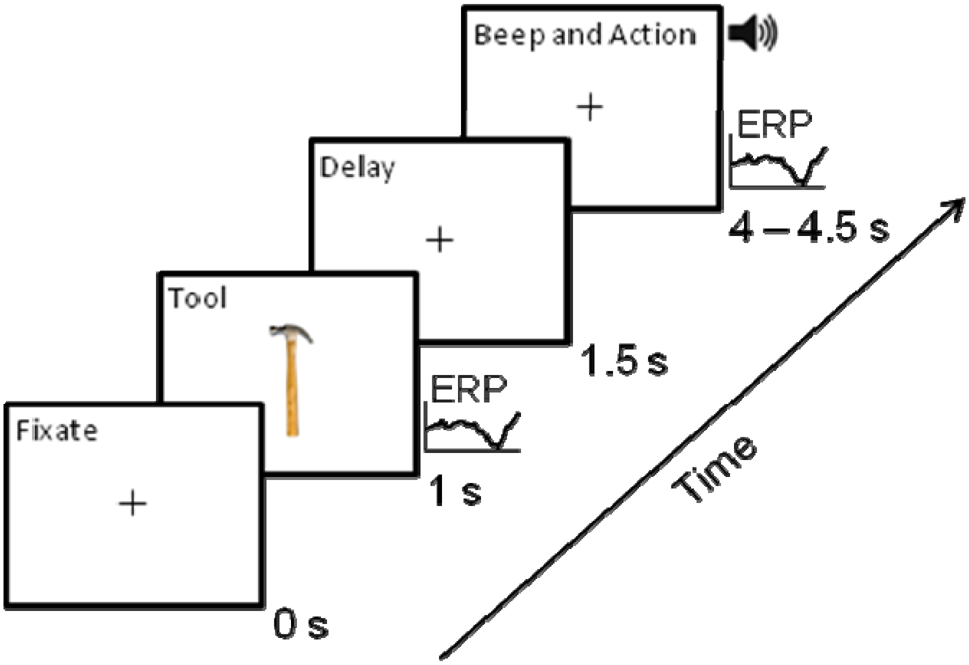

Figure 3-1 Delayed pantomime action paradigm
Participants were presented with a tool and, depending on the type of beep delivered after the delay period, either pantomimed using the tool (go) or did nothing (no-go). ERPs were collected at tool presentation onset and at beep onset. The times at the bottom-right of each screen indicate onset time relative to the start of the trial.

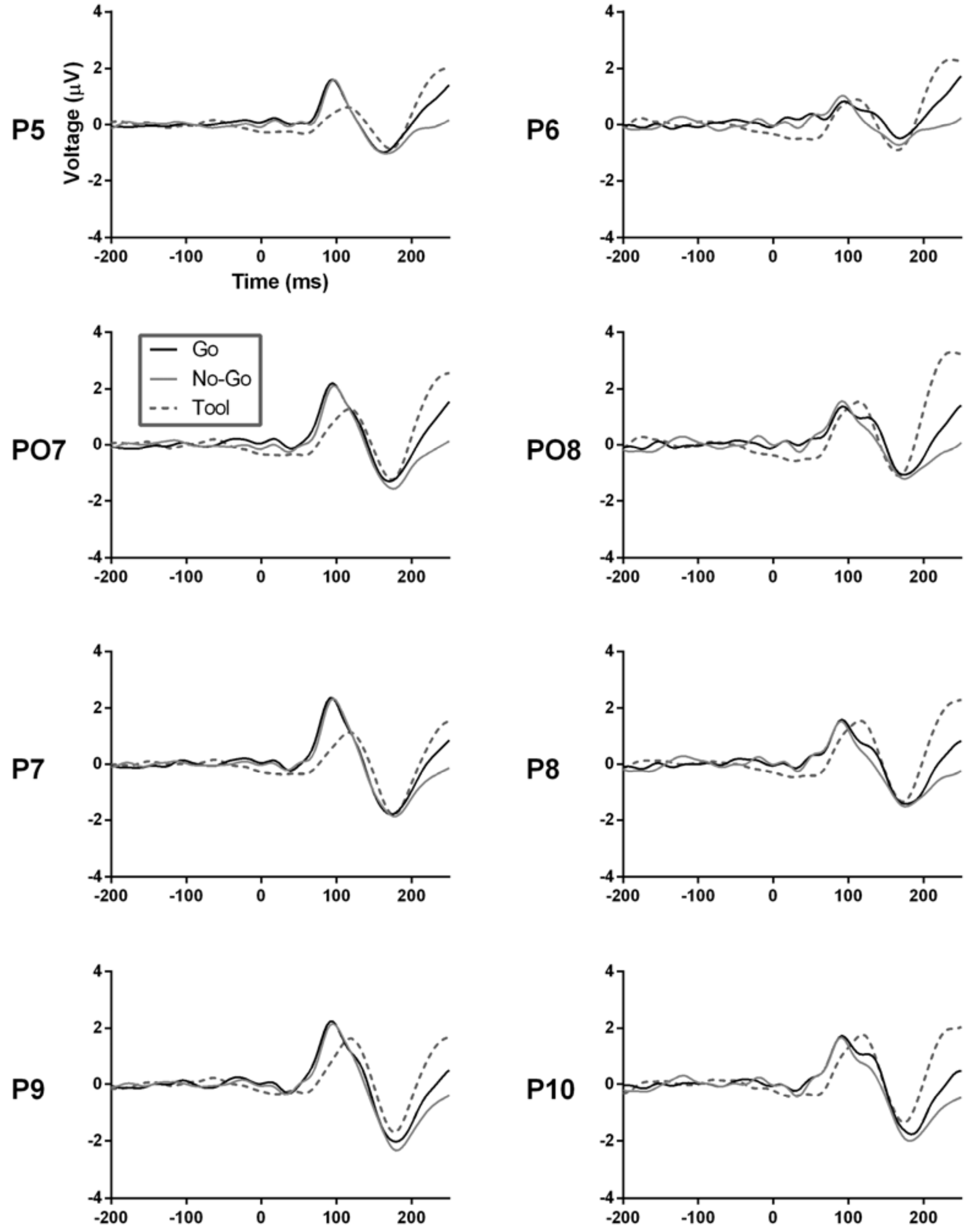

Figure 3-2 Go, no-go, and tool waveforms
Grand average waveforms from auditory go (solid black) and no-go (solid gray) beeps and tool presentation (dotted gray) at lateral occipito-temporal electrode sites.

Table 3-1 Mean N170 amplitude (in µV ± SE) for each condition at lateral occipito-temporal electrode sites

	Condition	
Electrode Site	Go	No-go
P5	-1.54 ± 0.30	-1.77 ± 0.34
PO7	-1.71 ± 0.34	-2.06 ± 0.39
P7	-2.17 ± 0.37	-2.35 ± 0.40
P9	-2.42 ± 0.41	-2.71 ± 0.44
P6	-0.95 ± 0.28	-1.32 ± 0.29
PO8	-1.49 ± 0.27	-1.72 ± 0.29
P8	-1.82 ± 0.30	-2.06 ± 0.34
P10	-2.14 ± 0.35	-2.52 ± 0.41

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4 General Discussion

The purpose of these two experiments was to investigate the attentional and perceptual mechanisms underlying visually guided and delayed actions. The first experiment measured ERPs in a cross-modal dual-task paradigm to investigate the attentional requirements of these two types of actions. In a primary joystick-controlled continuous reciprocal aiming task, participants moved a cursor back and forth between two targets of variable size in visually guided and memory-guided conditions. In a secondary dichotic listening task, ERPs were collected while infrequent high and frequent low pitch tones were delivered to both ears. Participants responded to the infrequent tones delivered to only one attended ear. Aiming and listening were performed separately and together as a dual task. I was interested in two ERP components: the P300 component, which reflects voluntary attention and perception, and the MMN, which reflects automatic attention. The results showed that the P300 component elicited by the auditory task was decreased in amplitude by the dual-task conditions compared with the auditory task alone. Moreover, P300 latency was increased by the memory-guided aiming condition, but not the visually guided aiming condition. On the other hand, the MMN component elicited by the auditory task was only attenuated by the visually guided aiming condition. Together, these results suggest that memory-guided aiming requires more voluntary attention and less automatic attention than visually guided aiming.

The first experiment, beyond characterizing the attentional requirements of visually guided and memory-guided actions, is also very interesting in what it can tell us about rhythmic actions. Unlike most studies of visually guided and memory-guided actions, which test discrete actions like reaching and grasping, this experiment used visually guided and memory-guided versions of a rhythmic action: continuously moving a cursor back and forth between two targets. This could be an important distinction because rhythmic movements activate less cortex than discrete movements (Schaal et al., 2004). With dual tasks using discrete actions there is usually reciprocal interference between the two tasks (Singhal et al., 2007), but in this experiment I observed only one-way interference. The introduction of the dichotic listening task did not impede rhythmic aiming. This suggests that rhythmic actions are more encapsulated than discrete actions.

Furthermore, the pattern of attentional results might be explained by the fact that a rhythmic action type was used. Behavioural studies of discrete visually guided actions have suggested that voluntary and involuntary attention are deployed maximally when the target to be acted on is presented at the same time as the cue to act on it (Deubel and Schneider, 2003; Wood et al., 2011). When participants are given time to preview the target, voluntary attention is much less taxed and there is no evidence of automatic attention biasing actions. In this aiming experiment, participants are given unlimited time to preview the stimuli. They see them for several seconds before the experiment starts, and they continue to see them throughout the experiment. Therefore, the findings that visually guided actions taxed both voluntary attention (seen by a decrease in P300 amplitude) and involuntary attention (seen by a decrease in MMN amplitude) would be very surprising if the actions were discrete. They may be explained by the rhythmic nature of the task, however. When participants preview a target in a discrete action task, they preview both the starting and ending points of their movement. Because they have time to absorb this information, less attention may be required when the action is cued to start. However, when participants preview the targets in the reciprocal aiming task, they only preview the end points; the starting point for each movement is different because it is determined by the end point of the previous movement. Every movement is different than the one before which may be why voluntary and involuntary attention are more dynamically employed throughout rhythmic action tasks.

An unresolved issue in this experiment is the relative contribution of object-related attention and spatial attention to the P300 latency effect in memory-guided aiming. Previous research has shown that memory-guided saccades have a spatial attention inhibitory effect at the target location (Ostendorf et al., 2003). However, the P300 is elicited by a type-selection process related to object-related attention. Unfortunately, I was not able to correlate the timing between the aiming task and the dichotic listening task. The two tasks started and ended at the same time, but were timed independently. Having this timing information could be very helpful in testing whether the P300 latency effect is due to spatial attention or object attention. For example, if dichotic listening performance deteriorated when memory-guided actions were initiated towards the attended side of space, it would be evidence that spatial attention is responsible for the P300 latency effect.

The second experiment tested if delayed pantomimed action planning employed perceptual processing, and tested if the N170 reflects this processing. ERPs were collected while participants were presented with pictures of tools and then, after a delay, either pantomimed how each tool was used (go) or did nothing (no-go). No differences in N170 amplitude were found between go and no-go trials. This result is at odds with the established literature. It does not correspond to Singhal et al.'s (2006) fMRI study that found ventral stream LOC activation for delayed actions. It does not correspond to Cruikshank et al.'s (2012) study finding greater N170 amplitude for delayed compared to immediate actions. It does not even correspond to the first experiment described in this paper, which found interactions between delayed actions and the perceptual P300 component.

In the previous chapter, I identified a number of reasons why there was no difference in N170 amplitude between go and no-go trials. However, when

Cruikshank et al.'s (2012) study is considered, many of these explanations seem unlikely. For example, it is not likely that the N170 occurs too early for a difference between go and no-go conditions to be seen when it occurs early enough for a difference between immediate and delayed conditions to be seen in Cruikshank's study. The most likely explanation for the failure to find differences go and no-go trials is that participants relied on long-term memories of the type of tools shown rather than remembering the particular images shown. To perform this delayed pantomimed task, no physical properties of the visual stimuli shown need to be remembered. The only information that needs to be extracted is what type of tool was shown and the rest can be forgotten. This is very different from Cruikshank's study where the position of each stimulus must be remembered. The N170 effect found in Cruikshank et al.'s (2012) study comes from participants accessing perceptual short term memories to perform delayed actions, but these memories do not need to be accessed in my experiment; long-term memories can be used instead.

4.1 Future Directions

This work has opened up several avenues of future attentional and perceptual research. The simplest follow-up would be to replicate the dual task experiment but co-register the timing of the aiming task and dichotic listening task. This would allow me to test if the direction of the memory-guided movement affects performance on the dichotic listening task. If it did, this would be evidence that memory-guided action interference is due to spatial attention.

I have attributed the surprising interactions between voluntary and involuntary attention and visually guided actions to the rhythmic nature of the actions used in the dual task experiment. However, this assumption can be tested. By comparing the pattern of ERP effects elicited by discrete and rhythmic actions in a similar dual task framework our understanding of the differences between these actions can be improved.

Finally, considering the limitations of the delayed pantomime experiment, it should be redone giving the participant different pantomime instructions. If participants were instructed to pantomime picking up and using the tool that was shown, they would have to remember the particular orientation the tool was presented in and the position of its handle in order to pantomime correctly. If N170 amplitude differences between go and no-go conditions were found, this experiment could be further modified to investigate how changing the duration of the delay period between target presentation and action, thereby changing the memory load, affects the N170 elicited by action planning (action N170). Perceptual representations degrade with time while action mechanisms stay constant. If N170 morphology correlates with delay time for delay periods often used in psychophysical studies of visual working memory: 0-10 s (Pasternak and Greenlee, 2005), this would suggest that the action N170 reflects perceptual memory. Furthermore, if the latency of the N170 elicited during action planning correlates with the time to initiate a delayed pantomimed action, this would be even stronger evidence that the perceptual mechanisms reflected by the N170 are critical in planning delayed actions.

4.2 References

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Appendices

Appendix A: Diagrams of analyzed electrodes

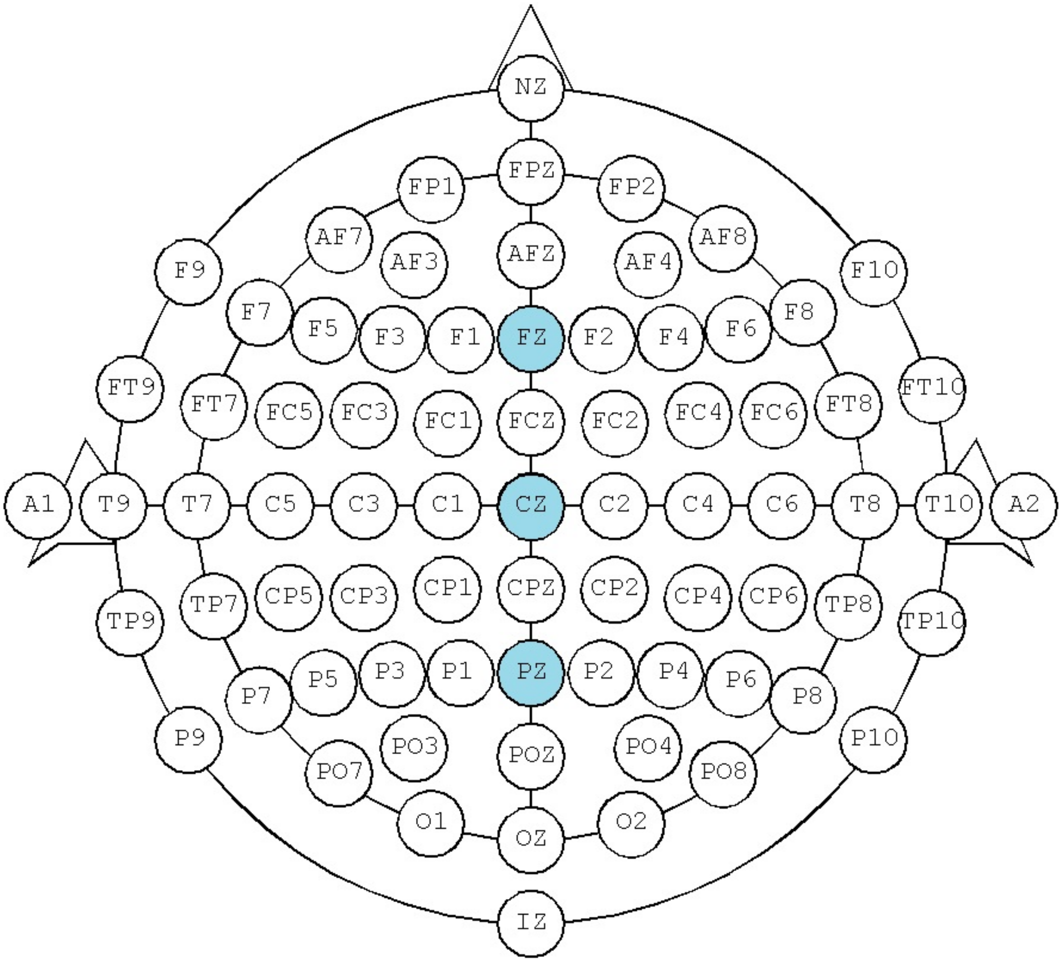

Figure A-1 Electrodes analyzed in experiment 1
Electrodes highlighted in blue, Fz, Cz, and Pz, were analyzed in experiment 1, neural markers of automatic and controlled attention during immediate and delayed action.

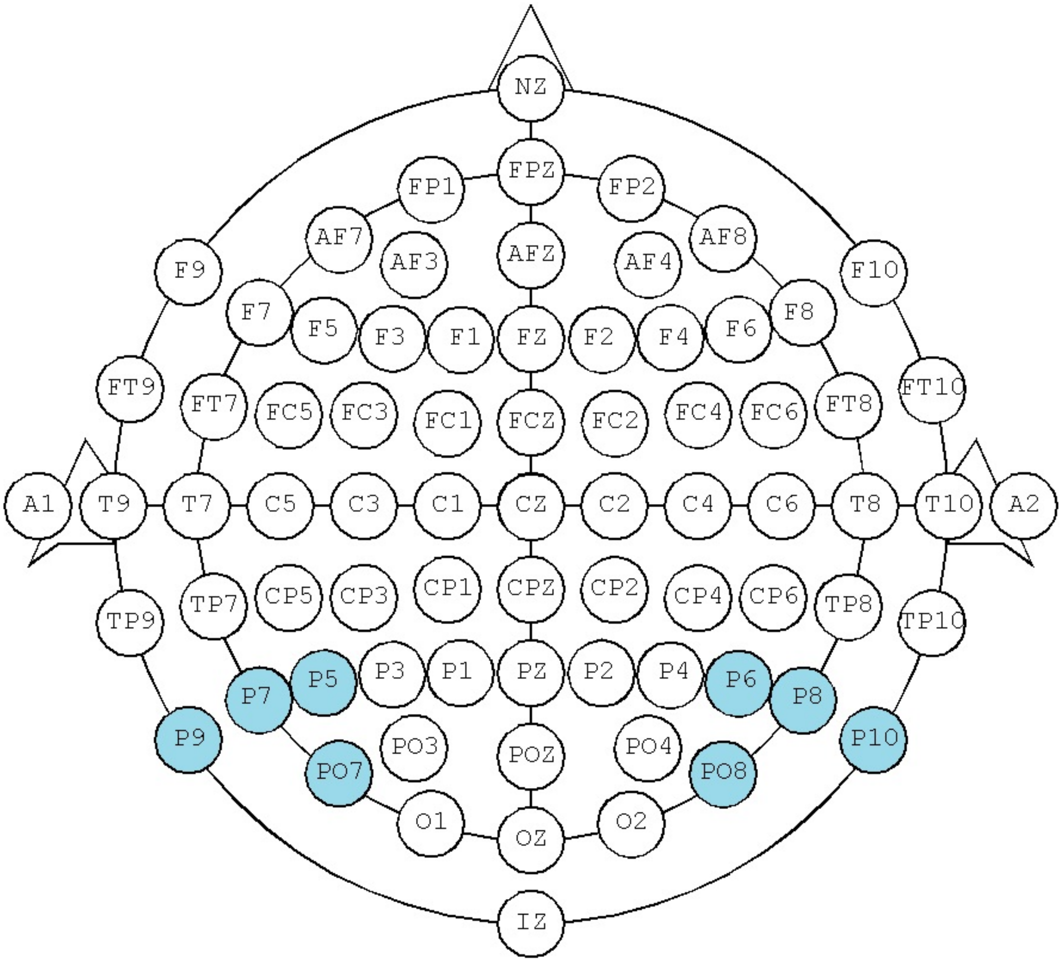

Figure A-2 Electrodes analyzed in experiment 2
Electrodes highlighted in blue, P5, P6, P7, P8, P9, P10, PO7, and PO8, were analyzed in experiment 2, perceptual mechanisms underlying delayed pantomimed actions.

Appendix B: Behavioural and ERP mean plots for neural markers of automatic and controlled attention during immediate and delayed action

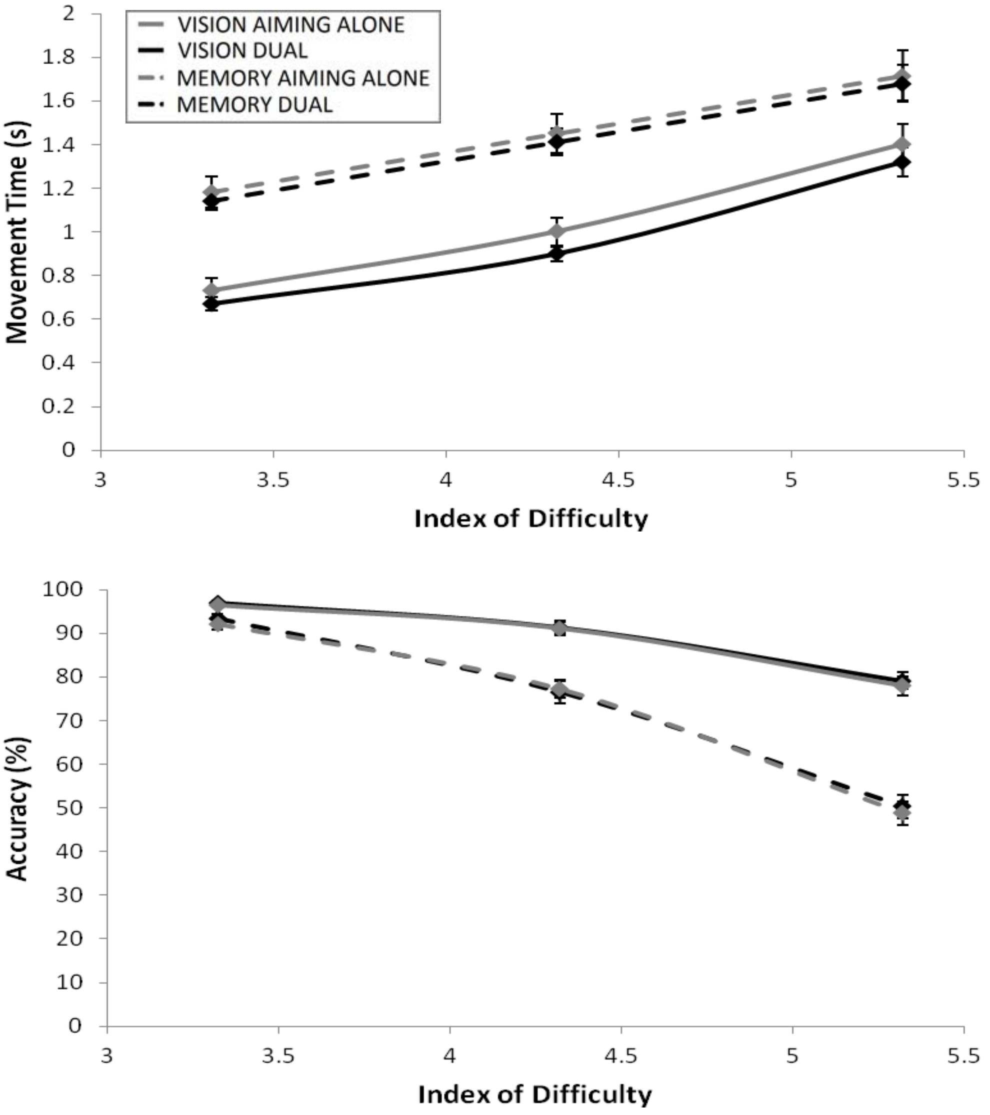

Figure B-1 Aiming task performance mean plots
Average movement time and accuracy (± standard error) for the visually guided and memory-guided aiming at each index of difficulty performed alone and together with the dichotic listening task.

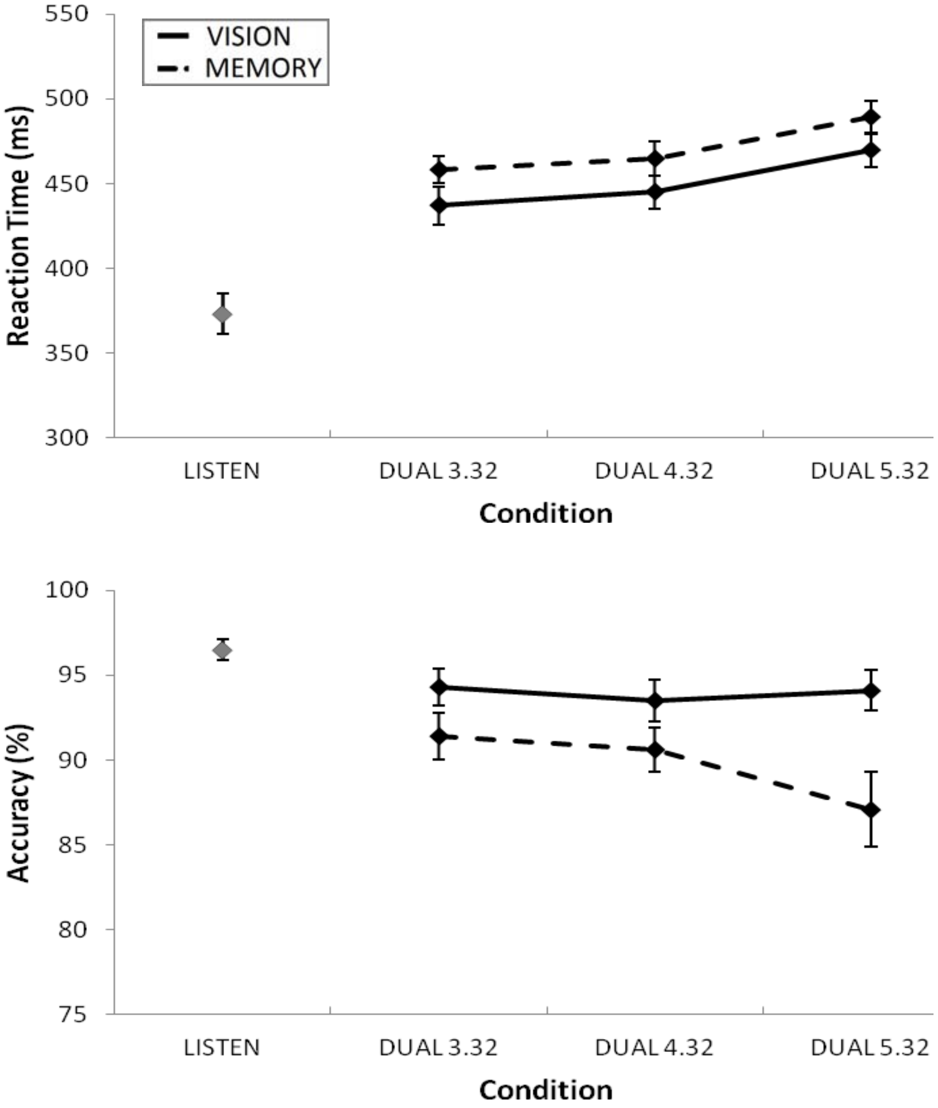

Figure B-2 Auditory task performance mean plots
Average reaction time and accuracy (± standard error) for the dichotic listening task performed alone and together with visually guided and memory-guided aiming at each index of difficulty. Error bars

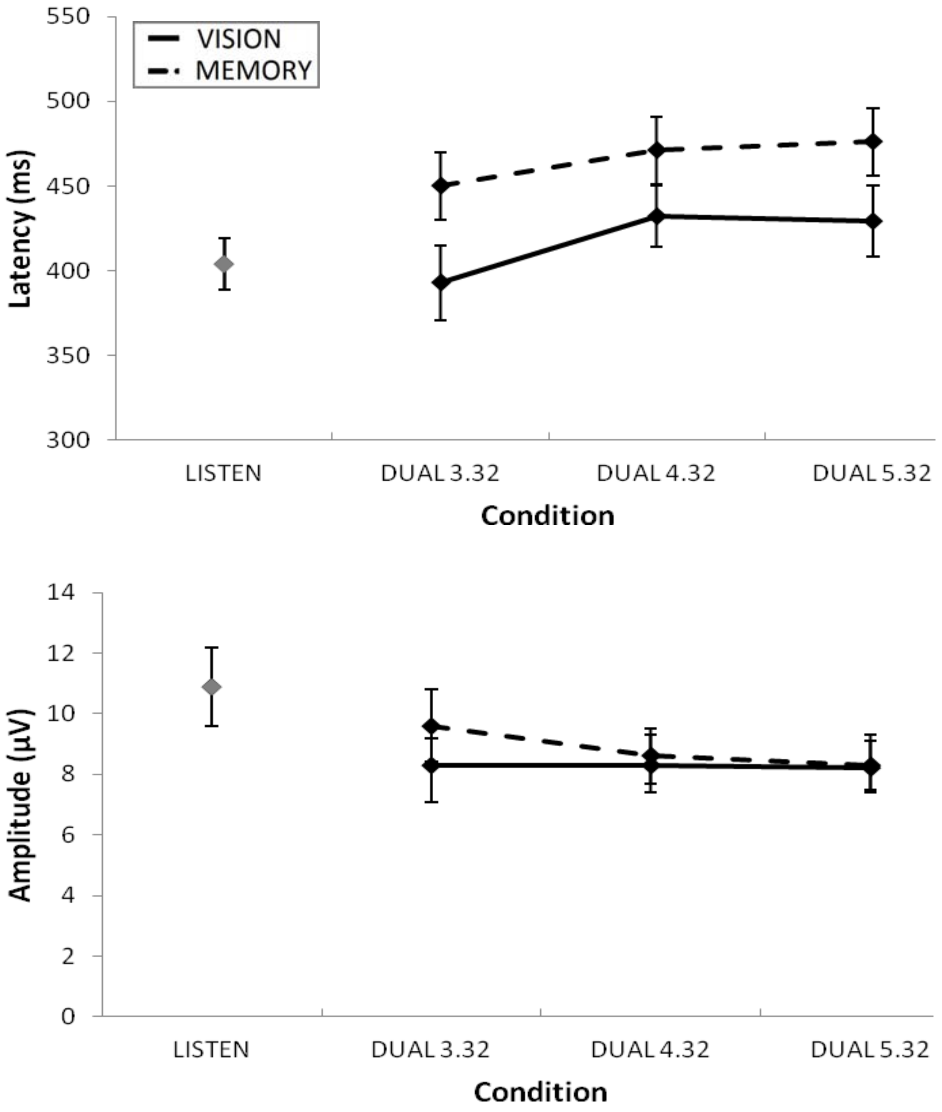

Figure B-3 P300 mean plots
Average latency and peak amplitude (± standard error) of the P300 at electrode Pz for the dichotic listening task performed alone and together with visually guided and memory-guided aiming at each index of difficulty.

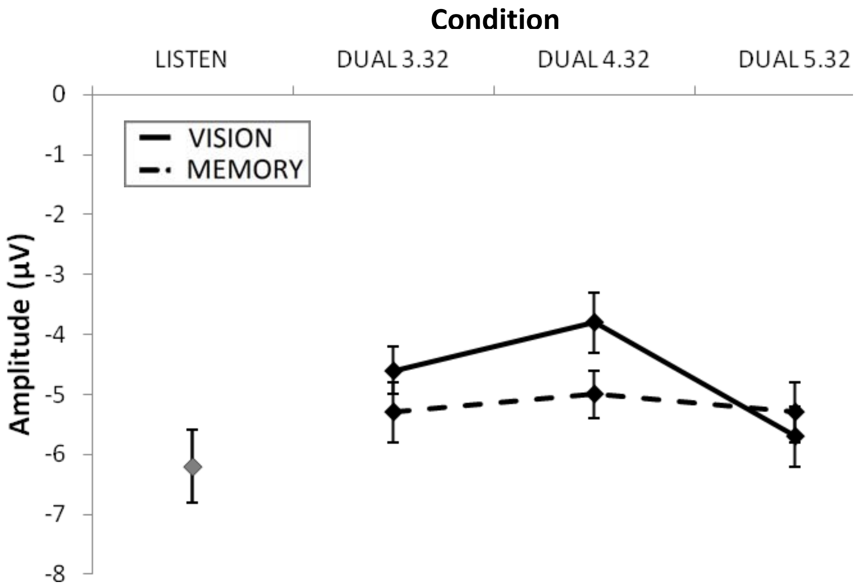

Figure B-4 MMN mean plot
Average peak amplitude (± standard error) of the MMN at electrode Cz for the dichotic listening task performed alone and together with visually guided and memory-guided aiming at each index of difficulty.