Mechanisms of action-modulated vision: behavioural and EEG investigations of motor-visual priming.

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A thesis submitted to the University of London for the degree of Doctor of Philosophy

Declaration of Authorship

I, Xavier Emmanuel Job, hereby declare that this thesis and the work presented in it is entirely my own. Where I have consulted the work of others, this is always clearly stated.

Signed: Date: 22/10/2018

Acknowledgements

My most sincere thanks go to my supervisors Jan de Fockert and José Van Velzen for all of their support and guidance throughout the years. Their wisdom, warmth and enthusiasm for research makes them the best mentors I could have hoped for.

I am also grateful to many members of staff in the Psychology Department at Goldsmiths. To Marinella Cappelletti, Joydeep Bhattacharya and Maria Herrojo Ruiz for their helpful discussions and insights. Also, to Rob Davis and Richard Smith for building so many of the response devices, without which this research would not have been possible.

Thanks also to my fellow Office Club members: Rhiannon Thomas, Mara Golemme, Natalie Bowling, Rachel Slavny, Giulia Orioli and Dan Brady for all of their friendship and support. A special thanks goes to Mara, whose collaboration has been invaluable — as have the Italian lessons, Christmas dinners, delicacies from The Box and so much more.

Thanks also to Joseph Walker, Thibault Uytterhaegen and Teemu Toivainen who have each in their own ways contributed to my journey through academia.

To my family, who have supported me in more ways than they or I know.

Finally, I would like to thank Hester. Your love and encouragement made it all possible.

Abstract

Perception and action have classically been understood as independent and isolated processes. More recent theories propose that action preparation may play a role in shaping the selection of perceptual information by prioritising action-relevant sensory information, suggesting a tight coupling between the two domains. However, the precise mechanisms underlying effects of action on perception are poorly understood, particularly regarding perception of non-spatial visual features. The experiments reported in this thesis investigate how the preparation of simple grasping actions influences the perception of stimulus properties including orientation, size and the hierarchical structure of objects (local/global processing), the latter of which is previously unstudied in the context of action preparation. Across the experiments, the typical behavioural effect emerged such that target stimuli were responded to faster if they contained a visual feature relevant to the upcoming action. Additionally, early brain responses (N1 event-related potential component) elicited by stimuli varying in their relative size were modulated by action preparation, suggesting action preparation affects already early sensory processing of a non-spatial feature. However, behavioural reaction time effects were not always found to reflect changes in early sensory processing. Instead, reaction time effects were reflected by changes in beta band (13-30Hz) synchronisation over sensorimotor brain regions, indicative of improved response preparation. Together, these findings show effects of action on perception may operate on early selection mechanisms under certain task conditions, but likely also operate on higher order decision and/or response processes. The results are discussed in terms of the wider theory regarding mechanisms of action-modulated visual processing.

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Chapter 1: GENERAL INTRODUCTION

1. Overview

Perception and action have classically been understood as independent processes and have therefore been studied largely in isolation. This has led to the assumption that information processing operates in a serial manner, beginning with perception of sensory information and ending with the execution of actions. More recent theories propose that perceptual and motor processes are much more integrated than previously believed. While it is rather intuitive that visual perception of an object can directly influence how you act upon that object, evidence now suggests that how you move can also affect what you perceive. Effects of action on perception are thought to reflect a top-down biasing of the sensory information relevant to a prepared action at the expense of less relevant sensory information.

Top-down modulations of perception are commonly attributed to mechanisms of attention, whereby sensory processing of task-relevant features is prioritised relative to less relevant features. In line with the notion that perception and action are tightly coupled, parallels have been drawn between mechanisms of attentional selection and the mechanisms supporting effects of action on perception. Some theories have taken this assertion even further and propose that attention is a direct derivative of the mechanisms serving the control of basic motor actions (Hommel, 2010; Rizzolatti & Craighero, 1998). These models therefore predict that action planning should result in enhanced processing of action-relevant perceptual features, reflecting a tight coupling between these two domains. Indeed, bidirectional links between action and perception have been observed, however the mechanisms underlying these effects are not clear.

This thesis first seeks to extend the understanding of the effects of action on perception to include the perception of the local and global structure of objects, features that have not yet directly been examined in the context of action preparation. Secondly, the neural mechanisms of action-modulated cognition are investigated more closely to ascertain whether the commonly reported effects of action planning on behavioural measures of perception reflect early stages of sensory processing associated with modulations in the sensory cortex. To do this, a combination of behavioural and electrophysiological measures is used.

Overall the results of the thesis reveal that action preparation may play a role in shaping incoming perceptual processing under certain task conditions. However, in some cases a behavioural 'motor-visual' priming effect can be found without evidence for modulations of early sensory processing. Rather than simply reflecting a biasing of early perceptual information, action more likely influences multiple processing stages to give rise to behavioural facilitation of action-relevant stimulus features.

In the remainder of this chapter a review of the existing theoretical models of action-modulated cognition is provided first. Following this, experimental evidence for influences of action on perception from the broader literature are reviewed, followed by a focus on motor-visual priming paradigms. At the end of the chapter, the specific research questions addressed in this thesis are described alongside relevant empirical evidence. Very broadly, these research questions seek firstly to provide evidence that action preparation can influence perceptual processing and secondly to investigate the neural mechanisms underlying such effects.

2. Theoretical background

It is well known that cognitive processing of objects in the environment is capacity limited. At any given time, there are severe limitations on our ability to attend to information (Egeth & Kahneman, 1975), retain items in short term memory (Luck & Vogel, 1997; Pashler, 1988; Todd & Marois, 2004) and to recognise items (Cherry, 1953) to mention only a few. The inability to process all of the incoming sensory information from our environment results in a requirement to optimally select only the most relevant information and to disregard less relevant information. Selection is therefore considered crucial for effectively perceiving and interacting with the external world. How exactly relevant information is selected at the expense of less relevant information has been a topic of interest for many years (e.g. James, 1890) and continues to be an active research field within cognitive psychology (for reviews see Carrasco, 2011; Driver, 2001).

2.1. Selection-for-perception, selection-for-action

In order to overcome the capacity limitations of the cognitive system, there is a necessity to select certain information from the environment at the expense of other information. The selection of sensory information is most often attributed to mechanisms of attention, a process of filtering relevant, from less relevant information. The ultimate purpose of an attentional system is classically understood as selecting certain sensory information for further perceptual processing, referred to as *selection-for-perception.* For example, attention is involved in orienting sensory perception toward stimuli for further processing (LaBerge & Brown, 1989; Posner, Snyder, & Davidson, 1980) in searching for target stimuli among distractors (Treisman & Gelade, 1980; Wolfe, Cave, & Franzel, 1989) as well as encoding and maintaining information in short term memory (Bundesen, 1990). The general goal of attentional selection in these cases is to prioritise the *perception* of certain sensory information.

Information may be selected, however, for another purpose. When planning simple actions, certain stimulus features may be regarded as more or less relevant to the upcoming action. Planning an action therefore also necessitates a process of sensory selection, which is considered essential for the effective planning and control of movements. The *selection-for-action* approach, first advocated by authors such as Allport (1987) and Neumann (1987), views attention as limited by action potentialities. The underlying assumptions of selection-for-action differ considerably from those of selection-for-perception. Selection-for-perception assumes that selection is required because of limitations in the amount of information that can be consciously represented at any one time. Selection-for-action, however, assumes that selection of information is required not because of a limit in the capacity of conscious awareness, but because of a limit on action potentialities. For example, we may select one apple among many on a tree not because of a limit on the number of apples that can be actively attended to, searched for or remembered, but because only one apple can be actively picked at one time. The selection-for-action approach therefore challenges the notion that capacity limitations prevent the 'overloading' of conscious awareness but instead reflect limitations in the action capabilities of an agent.

From a neurophysiological perspective, the distinction between selection-for-perception and selection-for-action is supported by the broad division of visual information processing in the brain into distinct neural pathways. A brief discussion of the two major pathways for visual information processing and their properties will be covered next.

2.2. Two pathways for visual information processing

Visual processing within the cerebral cortex can be broadly divided into two processing streams, or pathways (Ungerleider & Mishkin, 1982) known as the dorsal and ventral streams. The dorsal stream, extending from primary visual cortex (V1) to the posterior parietal cortex, is thought to compute information about the spatial properties of stimuli and was therefore termed the "where" pathway. The ventral stream, extending from V1 to the inferior temporal cortex, is thought to compute information related to the structural properties of stimuli and was therefore termed the "what" pathway. The broad characterization of the dorsal and ventral steams as processing visual information pertaining to the "where" and "what" of visual perception has been one of the most pervasive accounts of parallel information processing in vision.

Later extensions to the idea of multiple processing pathways in vision (Goodale & Milner, 1992; Milner & Goodale, 2008; Milner & Goodale, 2012) characterized the dorsal stream as responsible for the visual control of action ('vision-for-action') and the ventral steam as responsible for perceptual representations ('vision-for-perception'). This extension differs quite markedly from the original conception, as it assumes that the structural and spatial attributes of objects are processed by both streams, but for different purposes. In the ventral stream, the enduring features of objects are processed, forming long-term representations that play an important role in object identification, classification and the accumulation of object knowledge. In the dorsal stream, momentary information about stimulus features such as size, structure, location and motion are processed, which play a crucial role in the visual control of skilled actions (Milner & Goodale, 2012).

There is still an active debate surrounding the extent to which vision-for-perception and vision-for-action indeed represent functionally independent processes (Franz &

Gegenfurtner, 2008; Schenk & McIntosh, 2010; Westwood & Goodale, 2011). However, recent theories converge on understanding the perceptual system as playing a role in gathering and integrating sensory information in order to adapt to environmental changes resulting from actions taking place. This notion is reflected in many different models that assume a close relationship between visual attention and action systems. Among the most influential approaches are the *Premotor Theory of Attention* (Rizzolatti & Craighero, 1998) and the *Theory of Event Coding* (Hommel, Müsseler, Aschersleben, & Prinz, 2001) with its earlier formulations in ideomotor principles (James, 1890; Lotze, 1852).

2.3. Premotor theory of attention

The premotor theory of attention (Craighero & Rizzolatti, 2005; Rizzolatti, Riggio, Dascola, & Umiltá, 1987) challenges the classical notion that attention is a dedicated supramodal control mechanism that is anatomically distinct from the circuitry underlying sensorimotor processing (see Posner & Dehaene, 1994). According to the premotor theory, the brain circuitry responsible for the coding of spatial representations is also responsible for coding motor programs relevant for different effectors (i.e. eye, hand, arm). These mechanisms, responsible for both spatial representation and motor processing, are termed 'spatial pragmatic maps' and refer to dedicated dorsal brain structures primarily located in the primate inferior parietal lobule and pre-motor cortex. The theory then asserts that shifts of spatial attention occur as weaker activation of the circuitry controlling movements. In other words, attention is therefore viewed as deriving from the same fronto-parietal circuitry underlying motor actions.

Extensive evidence has supported the premotor theory's assertion for shared control mechanisms of attention and action. The initial focus was on the links between eye-movements and shifts of visual-spatial attention. Behavioural evidence showed that stimuli appearing at the target location of an upcoming saccadic eye-movement may receive preferential processing compared to the same stimuli presented at adjacent locations (Deubel & Schneider, 1996a; Hoffman & Subramaniam, 1995; Shepherd, Findlay, & Hockey, 1986). Subsequent neuroimaging evidence also found that overlapping brain areas were involved in tasks of visual-spatial attention and simple movements (Astafiev et al., 2003; Maurizio Corbetta et al., 1998a; Perry & Zeki, 2000).

Neurophysiological investigations with non-human primates have also shown that spatial attention and eye-movements rely on overlapping brain structures. For example, stimulation of frontal eye field (FEF) neurons results in saccades towards the receptive fields of the neurons stimulated (Schiller & Tehovnik, 2001). Furthermore, subthreshold stimulation of the same neurons facilitates target detection at those locations without causing saccades to be executed (Moore & Fallah, 2004). Analogous evidence in human subjects is made possible with the use of non-invasive techniques of brain stimulation. Stimulation of the FEF with transcranial magnetic stimulation (TMS) can result in the selective facilitation (Van Ettinger-Veenstra et al., 2009) or impairment (Neggers et al., 2007) of behavioural responses to targets presented at the location of upcoming saccades.

The premotor theory has been extended in several ways beyond its original conception. Most notably, spatially guided movements other than eye-movements are also accompanied by shifts of attention. Supporting evidence has shown that preparing pointing movements can facilitate target detection at the goal location of the movement (Deubel, Schneider, & Paprotta, 1998). Visual stimuli also elicit enhanced early event-related potential (ERPs) components when a manual movement is prepared at the same location, compared to preparing to move the adjacent hand (Eimer, Van Velzen, Gherri, & Press, 2006a; Gherri & Eimer, 2010). During the planning of reaching movements, stimuli presented at the goal location similarly elicit enhanced early ERP components, compared to the same stimuli presented at non-goal locations (Gherri, Van Velzen, & Eimer, 2009; Job, de Fockert, & van Velzen, 2016). Furthermore, similar effects have been found at the multiple goal locations of sequences of reaching movements (Baldauf & Deubel, 2009), as well as at effector and goal locations (Mason, Linnell, Davis, & Van Velzen, 2015). These findings suggest that the overlap between mechanisms of spatial attention and movement preparation is not limited to the 'spatial pragmatic maps' controlling eye-movements, but also those maps controlling other effectors.

The premotor theory was also extended from explaining the orienting of attention to spatial locations to the orienting of attention to objects. Studies on non-human primates showed that many neurons located in the monkey anterior intraparietal area (AIP) and premotor cortex (F5) would selectively discharge both when grasping an object and when viewing a graspable object (Rizzolatti & Luppino, 2001). Crucially, these neurons would only discharge when the properties of the object (size and shape) were congruent with the grasping action (precision and whole hand power grasping). This suggests that actions do not only result in an orienting towards action-relevant spatial locations, but also non-spatial object features.

In line with the view that action and the perception of object features is tightly coupled, extensive findings from human subjects have shown that simply viewing graspable objects can potentiate the associated grasping action (Symes, Ellis, & Tucker, 2005; Tucker & Ellis, 1998). In their seminal study, Tucker and Ellis (1998) used a stimulus-response compatibility paradigm in which subjects were presented with images of graspable objects and asked to respond with left or right keypresses if the images were upright or inverted. Reaction times were faster when the hand used to make the keypress response was most suited to grasp the presented object (see Borghi & Riggio, 2015 for a review of similar findings). Supporting evidence using neuroimaging has consistently shown that the observation of graspable objects is accompanied by activation of brain areas involved in object manipulation (Chao & Martin, 2000; Gazzola & Keysers, 2009; Grafton, Fadiga, Arbib, & Rizzolatti, 1997). Research using methods with more precise temporal resolution such as electroencephalography (EEG) and transcranial magnetic stimulation (TMS) have also investigated the time course of affordance effects. EEG studies have shown early modulations of activity evoked after the presentation of manipulatable, compared to non-manipulatable, objects (Proverbio, Adorni, & D'Aniello, 2011; Righi, Orlando, & Marzi, 2014; Rowe, Haenschel, Kosilo, & Yarrow, 2017), consistent with automatic object affordances in the motor system. Using TMS, studies have also shown enhanced excitability of cortical motor areas involved in grasping immediately following (within ~300ms) the visual presentation of graspable, compared to non-graspable objects (Buccino, Sato, Cattaneo, Rodà, & Riggio, 2009; Franca et al., 2012; Makris, Hadar, & Yarrow, 2011; McNair, Behrens, & Harris, 2017). Together, these findings show that the mere observation of manipulatable objects is accompanied by processing of the actions they afford.

2.4. *Common coding of action and perception*

Common coding approaches (Hommel et al., 2001; Prinz, 1990) view actions as coded in terms of the perceivable effects they generate. This approach is reminiscent of much earlier ideas (James, 1890; Lotze, 1852) that imagined actions can evoke a tendency to carry out those actions, now referred to as *ideomotor* interactions. If actions are assumed to be represented in terms of their perceptual effects, then perception and action necessarily share a common representational domain.

The theory of event coding (TEC, Hommel et al., 2001) is the most established of the common coding approaches. TEC holds that actions have the purpose of reaching certain goal states (intended action effects). Goals are acquired by actively learning associations between actions and their sensory effects. The 'bindings' between actions and their associated sensory outcomes provide the impetus for voluntary actions, such that the mere representation of an action goal (i.e. sensory state) is enough to activate motor programs needed to produce the action (Hommel, 2009; Shin, Proctor, & Capaldi, 2010). TEC therefore makes four core assumptions (Hommel et al., 2001).

1) Perceptual events and planned actions are represented by *event codes.*
2) Event codes are integrated assemblies of *feature codes.*
3) Feature codes are cognitive/brain states correlated with external (perceived or self-generated) features (*distal coding*).
4) The basic units of perception and action are *sensorimotor*, in the sense that they are activated by sensory input (perception) and controlling motor output (action).

According to this approach, the mechanism by which actions can influence perception is termed *intentional weighting* (Hommel et al., 2001; Hommel, 2010). This is the proposed mechanism by which stimulus processing of action relevant features is prioritised, or weighted, relative to non-action relevant features. Intentional weighting is thought to have developed in order to provide information for the open parameters of online action control (Hommel, 2010).

Both the premotor theory of attention and the theory of event coding clearly overlap in their explanatory power of the links between action and perception. The most notable overlap is their shared prediction of bidirectional links between processes of action and perception. For example, if perceptual and motor 'events' activate the same representational codes, then the perception of objects may activate associated actions, and planned actions may in turn activate perceptual representations of associated objects. However, there are some notable differences between the premotor theory of attention and common coding approaches such as TEC. In general, TEC is more of a 'functional' rather than structural or mechanistic theory, in the sense that it makes very few concrete predictions regarding brain processing. In contrast, the premotor theory of attention is more rooted in neurophysiology and therefore makes clear predictions about neural functioning and mechanisms underlying the links between action and attention. Furthermore, the premotor theory is primarily concerned, at least in its conception, with the links between spatial movements (eye-movements, reaching etc.) and attentional control of spatial representations. In contrast TEC has been more concerned with non-spatial stimulus features related to object processing.

Both theories propose tight bidirectional links between perception and action, such that perceived objects should automatically potentiate relevant actions, and prepared (or imagined) actions should also prime relevant perceptual features. The precise mechanisms of how action preparation modulates visual perception however, are not well understood. Given the known links between action and attention, discussed above, the mechanisms by which *action* influences perception may be analogous to the mechanisms underlying effects of *attention* on perception. Next, a brief overview of the mechanisms underlying effects of attention on sensory perception is provided.

2.5. Sensory gain as a mechanism of selection.

Perceptual processing is known to become biased towards task-relevant features or feature dimensions (Bundesen, 1990; Müller, Geyer, Zehetleitner, & Krummenacher, 2009; Wolfe, 1994). There is a broad consensus that this selection results from an attentional weighting of relevant perceptual features that biases the competition between perceptual representations (see Bundesen, 1990; Desimone & Duncan, 1995; Reynolds, Chelazzi, & Desimone, 1999). The mechanism underlying this selection is thought of as an amplification, or gain increase, of the neural populations coding for an attended stimulus. For example, attending to a stimulus feature dimension (e.g. colour or motion) causes increased neural responses in regions specialised for processing that particular attribute (Corbetta, Miezin, Dobmeyer & Schulman, 1990). Furthermore, ERPs evoked by visual stimuli are enhanced both when the luminance of the stimulus is increased, as well as when attention is directed towards that stimulus (Wijers, Lange & Mulder, 1997). Together, this suggests that the process of attending to a particular stimulus has direct effects on sensory perception. In other words, attention operates within the territory of perception, rather than outside of it.

If attentional selection operates within the territory of perception itself, and the mechanisms of attention and action planning are tightly coupled, then action planning and perceptual processing should be inextricably linked. This notion is formulated in the premotor theory of attention and echoed by common coding approaches to action and perception, described above. Evidence for sensory gain as a mechanism of *action-modulated* visual processing is currently lacking in the literature, with few investigations of the precise mechanisms of action modulated cognition. The existing experimental evidence for action-modulated cognition is described next.

3. Experimental evidence for action-modulated cognition

There have been many approaches to experimentally observe the coupling between the perceptual and action systems. These approaches differ in the types of inferences that can be drawn from their findings. The focus of this thesis is on motor-visual priming paradigms, which broadly seek to demonstrate effects of planning simple actions on processes of visual perception. However, motor-visual priming paradigms are not the only ways in which effects of action on perception have been investigated in the wider literature. Other approaches have manipulated the action *capability* of individuals or compared individuals with varying levels of action *expertise* (or impairments), as well as studying *learned* action-outcome associations. For completeness, a brief overview the wider experimental findings for action modulated cognition is provided, followed by findings from motor-visual priming paradigms more relevant to the research aims of this thesis.

3.1. Effects of action capability

A large number of studies have purportedly shown that subjective estimates of perceptual stimuli change when an individual's ability to act on those stimuli is restricted in some way. For example, hills can appear steeper when burdened with a heavy backpack (Bhalla & Proffitt, 1999; Proffitt, Stefanucci, Banton, & Epstein, 2003), targets are estimated as further away when throwing a heavy, compared to a light, ball (Witt, Proffitt, & Epstein, 2004), and objects appear closer to observers whose reach is elongated with a tool (Witt, Proffitt, & Epstein, 2005) to name just a few (see Witt, 2011). These effects are interpreted within the so called *action-specific account* of perception, which proposes that the environment is perceived in terms of an individual's *ability* to act within it (Proffitt, 2006; Witt, 2011). However, these claims have been rather controversial, provoking criticism about the possible origin of the effects (see Durgin et al., 2009; Firestone, 2013; Firestone & Scholl, 2014). The criticism most often levied at these studies questions whether they truly reflect influences on perception, or on response/decision related processes. This is because the focus in these paradigms is almost always on effects of action capability on explicit *judgements* of stimulus features, making it unclear whether effects reflect modulated perception, or merely response biases. Indeed paradigms investigating action capability are known to be highly susceptible to demand characteristics (Collier & Lawson, 2018), rendering their predictive power low.

3.2. Effects of motor expertise

Some studies have shown that action *knowledge* can lead to selective enhancements in perceptual sensitivity to actions and action effects. These studies typically investigate perception-of-action, to demonstrate how the perceptual system is tuned to one's own motor knowledge/capabilities. For example Calvo-Merino and colleagues (Calvo-Merino, Glaser, Grèzes, Passingham, & Haggard, 2005; see also Cross, Hamilton, & Grafton, 2006; Haslinger et al., 2005) compared expert classical ballet and capoeira dancers and found greater activity in premotor and parietal brain areas when dancers watched their own style of dance, compared to the other style. This was interpreted as a stronger engagement of the action system during the observation of actions which one has an extensive representation of.

Investigating functional impairments to one's motor system can also provide insights into influences of action on perception. For example, in two de-afferented individuals lacking cutaneous touch as well as proprioception, a selective deficit was observed for interpreting the observed movements of another person (Bosbach, Cole, Prinz, & Knoblich, 2005). When observing another person lifting boxes, these patients were unable to ascertain whether the actor had a false expectation regarding the weight of the box. Importantly, when asked to lift the box themselves, the patients were unable to attune their movements to their expectation of the weight of the box. This suggests that an individual's motor ability may be crucial for perceiving the observed movements of others.

3.3. Learned action-outcome associations

Some studies have taken the approach of building new associations between actions and effects through learning in order to investigate action perception coupling (e.g. Elsner & Hommel, 2001; Gozli & Ansorge, 2016). After learning that a sensory outcome reliably follows a particular action, the perceptual outcome is assumed to become an intrinsic part of the action. For instance, knocking on a door reliably results in associated tactile and auditory sensory outcomes, so the representation of the action then entails those associated tactile and auditory outcomes. Experimentally, in a task where keypresses are reliably followed by the presentation of tones with certain frequencies, new associations between actions (keypresses) and perceptual outcomes (tones) are formed (see Elsner & Hommel, 2001). In a subsequent task, this association can then be reversed, such that the presentation of a tone biases participants responses towards the associated action (a particular keypress), representing an automatic response priming through learned action-outcome associations.

In another study, a motor learning task was given before a visual task of discriminating biological motion patterns in point-light displays. Training participants to make novel arm movements resulted in an improvement in discriminating biological motion that matched the learned movements, compared to novel movements (Casile & Giese, 2006; see also Hecht, Vogt, & Prinz, 2001). Additionally, the better a participant could perform the movements in the training phase, the greater their advantage in the visual motion discrimination task. This suggests that proprioceptive representations of our own movements can influence perception of action. More generally, the findings from learned action-outcome association studies demonstrate evidence for the involvement of perceptual representations in motor execution and echo the notion that selecting an action involves anticipating the sensory consequences of the action.

Investigating relationships between different experimental phases (e.g. learning and test phases), or indeed differences between experts and novices, is useful for understanding how one acquires associations between perceptual and motor events. These approaches have therefore been important for understanding visuomotor processing as well as skill acquisition. However, these approaches are less well suited to investigating momentary effects of action planning on perception. Understanding how perceptual action-outcomes can become flexibly prioritised requires drawing inferences from more temporally sensitive demonstrations of action-modulated cognition. Motor-visual priming paradigms are more well suited to investigating such momentary effects of action on perceptual processing.

3.4. Motor-visual priming

Motor-visual priming paradigms seek to experimentally manipulate a participant's action state while simultaneously measuring visual processing. In a typical motor-visual priming task the participant is instructed to prepare one of two movements which vary on a particular feature, for example a rightward or leftward oriented grasping action. Importantly, the participant must withhold execution of the movement until instructed to do so. While the participant is preparing the movement, a visual stimulus must be detected. This stimulus either shares a feature with the prepared action or not, for example a stimulus that is oriented either rightward or leftward. Reaction times in response to the stimulus are compared for trials in which a congruent or incongruent action was prepared. Observed differences in reaction times are then interpreted as an influence of preparing a given action, on the perceptual processing of the visual stimulus. In other words, the processing of a visual feature is primed by the preparation of a particular action.

Motor-visual priming effects differ considerably from the aforementioned approaches of studying motor expertise or learned action-outcome associations. Rather than comparing groups differing on their level of motor expertise, priming effects allow for a more temporally precise assessment of perceptual processing during the various stages of planning and executing a movement. Movements can also be more easily manipulated in a within-subjects manner in motor-visual priming paradigms, thus reducing unwanted between-subjects variance. Effects of learned action-outcome associations are also suboptimal for investigating the online modulation of perception by action, as they necessarily require a learning phase in which new stimulus-response associations are formed. In contrast, motor-visual priming paradigms draw upon pre-existing stimulus-response associations to investigate the dynamic reallocation of perceptual resources in the context of action preparation.

One of the earliest motor-visual priming paradigms (Craighero, Fadiga, Rizzolatti, & Umilta, 1999) cued participants to prepare a grasping action toward an oriented bar and to execute the action as fast as possible after the presentation of visual stimulus. The visual stimulus was also a bar, which could be oriented either in the same direction as the prepared action (congruent) or in the opposite direction (incongruent). Grasping reaction times were faster to congruent, compared to incongruent visual stimuli. This finding was interpreted as evidence that preparing to act upon an object produces faster processing of stimuli congruent with that object, thus representing the tight coupling between processes of action and perception. Similar motor-visual priming effects have also been observed for features such as stimulus size (Fagioli, Hommel, & Schubotz, 2007; Symes, Tucker, Ellis, Vainio, & Ottoboni, 2008; Wykowska, Hommel, & Schubö, 2011; Wykowska, Schubö, & Hommel, 2009; Wykowska & Schubö, 2012), location (Collins, Schicke, & Röder, 2008; Deubel et al., 1998), and apparent motion (Lindemann & Bekkering, 2009).

Interestingly, a number of motor-visual priming studies have reported that actions can also interfere with the perception of a stimulus that shares a feature with the action (Müsseler & Hommel, 1997; Zwickel, Grosjean, & Prinz, 2007, 2008, 2010). For example in Müsseler and Hommel's (1997) study, participants prepared right or left key press responses and were subsequently presented with masked leftward or rightward arrow stimuli. Identification of the arrows was reduced when the prepared action was congruent with the arrow's direction, compared to incongruent (for similar interference effects see Zwickel and colleagues, 2008; Cardoso-Leite and colleagues, 2010). Interference effects such as these are typically interpreted within a common-coding framework (Hommel, Müsseler, Aschersleben, & Prinz, 2001; Prinz, 1997) as reflecting a binding of perceptual event representations into action plans, rendering them less available for processing by a secondary perceptual task (Hommel, 2004; Thomaschke, Hopkins, & Miall, 2012). This may seem at odds with demonstrations of facilitated processing of grasp congruent perceptual stimuli (e.g. Craighero et al., 1999; Lindemann & Bekkering, 2009), however a number of factors may determine whether a prepared action facilitates, or interferes with ongoing perception (for reviews of this topic see Thomaschke et al., 2012; Zwickel & Prinz, 2012).

One factor known to determine the direction of effect is the task-relevance of the perceptual feature of interest. In studies observing facilitation effects the perceptual feature that matches the action (e.g. grasp orientation and stimulus orientation) is typically task-irrelevant, in the sense that participants are not required to report the identity of that feature. However, studies that observe interference effects typically require participants to report the identity of the overlapping feature (e.g. report whether the arrow was leftward or rightward pointing in Müsseler and Hommel's (1997) task). This is in line with the notion that action planning results in a binding of relevant perceptual features, thus preventing their access by a secondary task (Hommel et al., 2001). When the overlapping feature in the secondary task is task-irrelevant and therefore merely incidental, a facilitation effect is expected.

Furthermore, a recent model of motor-visual priming (Thomaschke et al., 2012) highlights the importance of the control of visual information defined on *categorical* versus *metric* levels. For example, the stimulus-response consistency between left/right key press actions and centrally presented left/right arrow stimuli is defined on a categorical, non-spatial, level. However, planning a reach to grasp action requires online control of more precise spatial representations defined on a metric scale. Features defined on a categorical, rather than metric, level are thought to become bound into a stable action plan, and thus 'shielded' from further processing (Thomaschke et al., 2012). Therefore, interference effects are expected when actions such as left/right key presses are cued, and categorical perceptual representations are probed, such as centrally presented left/right arrow stimuli. However, facilitation effects may be expected in tasks that cue reaching and grasping actions, as these are likely to be guided by spatially specific perceptual information such as the precise goal location as well as the optimal orientation and aperture of the grasping action.

4. Thesis aims and research questions

The experiments reported in this thesis all investigate the influence of planning simple actions on visual perception, however the individual research questions can be broadly divided into two overarching aims. Firstly, experiments seek to test whether action preparation influences hierarchical stimulus processing, a perceptual feature dimension previously unstudied in the context of action preparation. Secondly, perceptual features more well known to be influenced by action preparation (stimulus size and orientation) are studied in order reveal the underlying neural mechanisms of effects of action on perception. To reach these aims, a combination of behavioural and electrophysiological measures is used.

Following an outline of the experimental methods in Chapter 2, two behavioural experiments are reported in Chapter 3 that investigate the processing of local and global stimulus features during the planning of precision and power grasping actions (pilot studies leading up to these experiments are also described in the Appendix). In Chapter 4, electrophysiological measures are used to investigate the processing of stimulus size during the planning of power and precision grasping actions, as well as an additional behavioural investigation of local and global processing. In Chapter 5, three behavioural experiments investigate the perception of stimulus orientation during the planning of oriented reach-to-grasp actions. In Chapter 6 electrophysiological measures are used to further investigate the perception of stimulus orientation during reach-to-grasp actions. A more detailed description of the background literature as well as the specific research questions addressed is provided next.

4.1. *Local elements and global wholes as action-relevant features*

The visual environment is intrinsically organised in a hierarchical fashion, with stimulus properties consisting of information about the *global* form of objects and the fine-grained *local* details (Navon, 1977). For example, leaves are nested within trees which are themselves nested within forests. Visual information can therefore be divided into local (elements) and global (whole) features. In order to effectively perceive and interact with the environment, visual information pertaining to both local and global features must be effectively represented, as well as optimally switched between. Studies have typically used hierarchical stimuli (Navon, 1977) in which a collection of local elements (often alphanumeric characters) are spatially arranged to form a global object (again typically an alphanumeric character). Participants then make speeded responses to target objects (e.g. the letter 'N') that can appear as either the local elements or the global whole. Initial findings supported a selective advantage for the processing of the global features of hierarchical stimuli with faster responses to the global, compared to local, features as well as greater interference from the global features (Navon, 1977). However, the advantage for global information can easily be reversed into a local advantage with experimental manipulations of visual angle, the number of local elements, retinal locus or shape (Hughes, Fendrich, & Reuter-Lorenz, 1990; Lamb & Robertson, 1988)

Many manipulatable objects in our environment can be thought of as having local and global features, which are potentially relevant for our interactions with those objects. For example, consider the branch of a tree with many leaves attached. The ('local') leaves can be picked with a precision grasp or the ('global') branch itself can be grasped with a whole hand power grasp. Similarly, a pot of pens may be acted upon by plucking a ('local') pen or grasping the whole ('global') pot. A single ('local') page of book may be turned with a delicate precision grip or the whole ('global') book may be clutched with a power grasp. The list of examples could continue, but the general idea is that many manipulatable objects can be seen to have local and global elements with which one can differentially act upon, particularly with either precision or power grasping actions. The division of manual grasping actions into 'precision' and 'power' grasps is supported not only from a functional perspective, but also from a phylogenetic and developmental perspective, as precision grasping emerged much later than power grasping both evolutionarily (Napier, 1956) and developmentally (Halverson, 1931). Therefore, while humans may be capable of displaying an exquisite degree of dexterity in their manipulation of objects, the vast majority of human grasping patterns can been divided in precision and power grasps (Napier, 1956).

Studies of motor-visual priming seek to demonstrate that preparing simple actions can result in a biasing of visual information that is relevant to the given action. For example, preparing to reach out and grasp an object may render a perceptual feature such as an object's location, orientation, size or apparent motion as relevant. Given the hierarchical structure of many manipulatable objects, the local and global features of objects may also become relevant during the preparation of grasping actions, just as features such as location, orientation and size are. However, to date there is no direct evidence that the hierarchical structure of objects is indeed an action-relevant perceptual feature. Interestingly, recent findings from three rather separate branches of research point toward this hypothesis, which are described next. In brief, the first concerns a similar pattern of hemispheric asymmetry that exists for local/global processing and precision/power grasping. Secondly, recent evidence from studies of 'near-hand' effects as well as object affordance effects similarly suggest a coupling between grasping actions and visual processing of hierarchical structure. In order to provide a basis for the hypothesis that hierarchical stimulus features may be action-relevant, each of these findings is described next.

There is considerable evidence that local and global processing is specialised to the left and right cerebral hemispheres, respectively. Evidence from behavioural (Hübner, 1998; Van Kleeck, 1989) as well as brain imaging studies using positron emission tomography (Fink, Marshall, Halligan, & Dolan, 1998), functional magnetic resonance imaging (Fink et al., 1996; Fink et al., 1997) and electrophysiological measures (Evans, Shedden, Hevenor, & Hahn, 2000; Malinowski, Hübner, Keil, & Gruber, 2002) converge on the relative lateralisation of global (right hemisphere) and local (left hemisphere) processing. Interestingly, evidence also suggests that precision and power grasping actions are also specialised to the left and right hemispheres, respectively. For example observational studies have found a preference for precision grasping with the right hand, irrespective of handedness in both non-human primates (Hopkins, Russell, Hook, Braccini, & Schapiro, 2005; Hopkins, Wesley, Cantalupo, Hostetter, & Pilcher, 2002) as well as human subjects (Gonzalez, 2006; Gonzalez, Whitwell, Morrissey, Ganel, & Goodale, 2007). Also, observing bi-manual object manipulation, Guiard (1987) observed that the left hand typically holds an object with a power grasp, while the right hand holds it with a precision grasp. Beyond observational studies, some have also reported faster left hand responses to large objects and faster right hand responses to small objects only when responding with a right hand precision grasp (engaging left hemisphere motor cortex) and a left hand power grasp (engaging right hemisphere motor cortex), however the effect disappeared when reversing these response types (Vainio, Ellis, Tucker, & Symes, 2006). Moreover, others have shown that instructing participants to make unilateral hand contractions to activate the right and left motor cortices resulted in a facilitation of global and local stimulus processing, respectively (Gable, Poole, & Cook, 2013). However, the mere observation of similar patterns of hemispheric asymmetry alone does not provide evidence for a functional relationship between local/global processing and precision/power grasping.

In another line of research, there has been a recent surge in findings that demonstrate differential effects on perceptual processing for stimuli that are presented near to, compared to far from, the hands (e.g. Davoli, Brockmole, Du, & Abrams, 2012; Langerak, La Mantia, & Brown, 2013; Thomas, 2015, for a review see Goodhew, Edwards, Ferber, & Pratt, 2015). For example in a recent study, Thomas (2015) had participants place their hands near to the presentation of visual stimuli either in a power grasp posture, a precision grasp posture or placed far from the stimuli. The power grasp posture facilitated performance on a global motion-detection task, while the precision posture facilitated performance on the global form-detection task. This suggests that different stimulus features (global motion or global form) can be differently weighted based on an observer's current affordances for specific actions. These effects are most often interpreted as a facilitation of visual perceptual information that is evaluated as potential candidates for action (Gozli, West, & Pratt, 2012; Makin, Holmes, Brozzoli, & Farnè, 2012; Reed, Betz, Garza, & Roberts, 2010). Interestingly, a recent study found faster responses to discriminate targets at the global level of a hierarchical stimulus when stimuli were presented near to the left hand, compared to the right hand or in an absent hand condition (Langerak et al., 2013). Left hand presence near to the stimulus may have improved global target discrimination, an ostensibly right-hemisphere process. Another study demonstrated that switching between local and global processing was markedly slower when the hand was in near proximity to the stimuli, compared to far (Davoli et al., 2012). Together, these findings suggest that local and global stimulus features may be differentially processed when they appear in close proximity to an effector, presumably because their properties are evaluated as potential candidates for action.

A similar pattern of hemispheric asymmetry, coupled with effects of placing hands near to local/global stimuli, provides only very indirect evidence for links between action and local/global processing. Inferences cannot be drawn from this rather indirect evidence alone. One other line of research has provided evidence for a more direct relationship between action and local/global processing. As discussed previously, the mere presentation of a task-irrelevant object feature has been shown to automatically prime actions associated with those stimuli, effects known as *object affordances* (Tucker & Ellis, 2004). Some evidence for local and global object affordance effects have emerged in the literature (Vainio, Ellis, Tucker, & Symes, 2007). This was based initially on series of experiments (Gentilucci, 2002) in which subjects were required to make precision grasping actions towards the 'local' element of 'global' objects (the stalks of fruits). Participants' maximum grasp aperture was found to be larger when the (task-irrelevant) global feature of the object was larger compared to smaller (e.g. apple vs. strawberry), suggesting that the global features of objects interfere with grasps towards the local elements of those objects. In a similar study (Vainio et al., 2007), right hand responses to the 'local' component of an object (e.g. the stalk of a fruit) were faster when it was part of a precision graspable 'global' object (e.g. strawberry) while left hand responses to the same local object were facilitated when it as part of a power-graspable global object (i.e. an apple). Firstly, these findings support the notion that precision and power grasping is to some extent specialised to the left and right hemispheres, respectively. Secondly the findings together suggest that the local and global features of objects may automatically prime precision and power grasping actions, respectively.

Object affordance effects are *visual-motor* in nature, such that the presentation of a visual object is found to automatically prime specific motor responses. In contrast motor-visual priming effects can be thought of as the reverse of this, where a prepared action primes the perception of a specific stimulus feature. If local and global features of objects automatically potentiate precision and power grasping actions, and the links between action planning and stimulus processing are bidirectional, then action planning should result in systematic influences on the visual processing of local and global stimulus features. The research questions addressed in Chapters 3 and 4 aim to further the understanding of the coupling between perception and action regarding local/global stimulus features. A motor-visual priming paradigm is used in which participants prepare precision or power grasping actions and subsequently detect a visual target that appears either at the local or the global level of a hierarchical stimulus (see Chapter 2 for further details of the experimental methods used).

4.2. Mechanisms of action-modulated visual processing

In Chapters 4-6, the mechanisms underlying effects of planning simple grasping actions on visual information processing are investigated. In particular, whether action planning influences early visual processing, as predicted by prominent models of action-perception coupling (Hommel, Müsseler, Aschersleben, & Prinz, 2001; Rizzolatti, Riggio, & Sheliga, 1994; Thomaschke et al., 2012), is tested using a combination of behavioural and electrophysiological measures. The perceptual features of size (Chapter 4) and orientation (Chapters 5-6) are studied as these features are well known to be relevant during manual grasping actions. Indeed there is strong evidence that the visual objects can prime the execution of actions if the object's size (e.g. Tucker & Ellis, 2001; Tucker & Ellis, 2004) or orientation (Symes, Ellis, & Tucker, 2007) affords grasping those actions. As described previously, the priming of actions by presenting objects, known as object affordance effects, can be thought of as the reverse of motor-visual priming effects, where perceptual processing is primed by prepared actions.

Behavioural motor-visual priming studies have shown that stimuli are responded to faster if they are oriented in the same direction as a prepared grasping action (Craighero et al., 1999), or if the stimuli's relative size is consistent with the prepared grasping action (Symes et al., 2008). Similarly, stimuli are detected faster if they appear to rotate in the same direction as a manual object rotation (Lindemann & Bekkering, 2009). These findings show that prepared actions can speed responses to action-relevant stimulus features, suggesting that sensory perception of those features is prioritised. However, speeded motor responses may not necessarily reflect changes to sensory perception but may instead reflect changes to a number of post-perceptual processes. For example, faster reaction times could reflect increased willingness of a participant to respond to a stimulus or increased certainty in their decision making regarding a stimulus (Pashler, Johnston, & Ruthruff, 2001)

If the effect of action on perception operates at the level of sensory perception, then preparing an action should influence an observer's sensitivity to discriminate the action-relevant feature. Unlike reaction times, signal detection measures of sensitivity (i.e. *d'*) reflect an observer's ability to discern a sensory event from noise, thus providing a more unambiguous measure of sensory processing (Green & Swets, 1966). Analysis of perceptual sensitivity, as well as accuracy in general is often precluded in motor-visual priming paradigms due to the use of relatively easy tasks of stimulus detection that garner error rates too low to meaningfully analyse.

In Chapter 5 and 6 perceptual sensitivity as well as speeded responses to discriminate stimuli that share a feature with a prepared action are investigated. Unlike many previous studies, to ensure uniform error rates the difficulty of the perceptual discrimination is continually updated throughout the tasks depending on each participant's performance. If action preparation alters visual perception of action-congruent stimulus features, then sensitivity to discriminate those features, as well as the speed of responses, should be facilitated relative to action-incongruent features.

It should be noted that in related set of paradigms perceptual sensitivity in the context of action preparation has been investigated. In these tasks, different types of manual actions are typically prepared (e.g. grasping, reaching or pointing), and participants simultaneously discriminate small changes in stimulus feature *dimensions* such as size, orientation or colour. In some cases, these studies have concluded that action planning not only speed responses, but also sharpens estimations of stimulus size (Bosco, Daniele, & Fattori, 2017; Fagioli et al., 2007) and orientation (Gutteling, Kenemans, & Neggers, 2011). However, these studies have focused on priming feature perception at a more general *dimension* level while preparing or executing qualitatively different types of actions (e.g. grasping or pointing actions). These effects tap into how the planning and execution of the invariant characteristics of a movement (i.e. select *what* action should be executed such as a non-specific reach or a grasp action) affects the weighting of feature dimensions in visual search. However, the more fine-grained variant characteristics of specific actions (i.e. prepare *how* an action should be accomplished such as a specific grasp orientation) may also affect concurrent visual processing. For example, before reaching out and grasping an object, perceptual information related to the specific size of the object should be selectively processed in order to adaptively guide the correct grasp aperture. In other words, previous studies have focused on effects of planning or executing qualitatively different actions (reach vs. grasp) on how one searches among feature *dimensions.* However, in most cases we select, plan and execute specific actions varying in their characteristics (e.g. reach location, grasp magnitude or grasp orientation), for which *specific* stimulus features may be relevant for. The distinction between processes of selecting 'what' action to plan, and specifying ‘how’ to accomplish an intended action is discussed further in Westwood and Goodale (2001).

Measures of neuronal activity with fine temporal resolution such as EEG can reveal whether effects of action on perception indeed reflect early sensory biases. There are surprisingly few EEG studies of motor-visual priming, with mixed patterns of results. For example, Wykowska & Schubö (2012) combined visual search tasks for size or luminance targets with motor tasks of grasping and pointing while recording EEG. They observed that pointing (compared to grasping) facilitated search times for luminance targets, while grasping (compared to pointing) facilitated search times for size targets. However early ERP effects were observed only for luminance targets, such that the P1 component (70-130 ms) was enhanced during pointing compared to grasping, but no P1 modulation was observed for size targets; instead a later effect on the N2pc component (230-300 ms), an ERP marker of spatial attention, emerged for size targets.

EEG is used in Chapters 4 and 6 to investigate the effects of grasp preparation on processing of visual size and orientation, respectively, aiming to directly demonstrate a selective effect of grasp preparation on early visual perception. In visual processing, enhanced ERP components have been observed in response to a task-irrelevant visual probe stimulus presented in an attended area relative to an unattended area of space (Hillyard, Vogel, & Luck, 1998; Hillyard & Anllo-Vento, 1998). Similar effects have been observed at the goal location of eye-movements (Eimer et al., 2006a; Eimer, Velzen, Gherri, & Press, 2007) and at effector and goal locations of reaching movements during movement preparation (Gherri et al., 2009; Job, de Fockert, & van Velzen, 2016; Mason et al., 2015) reflecting adaptive modulation of sensory processing tailored to the specific movement being prepared. Recent data suggest that the early sensory ERP components

(P1/N1) can also reflect a biasing mechanism operating on processing of other stimulus features, not just spatial locations (Karayanidis & Michie, 1997; Valdes-Sosa, Bobes, Rodriguez, & Pinilla, 1998; Zhang & Luck, 2009). If the behavioural effects of grasp preparation reflect a similar adaptive sensory modulation, then early event-related potentials elicited by visual stimuli should be modulated in line with the stimuli's compatibility with the prepared grasp.

Chapter 2: EXPERIMENTAL METHODS

1. Behavioural effects of action on perception

The vast majority of cognitive psychology tasks can be generally regarded as visual-motor paradigms, as they broadly attempt to manipulate the presentation of a stimulus, as an independent variable, and subsequently measure the participant's response, as a dependent variable. The underlying logic is that causal effects of stimuli on responses will manifest as systematic differences in measured responses as a function of the stimulus manipulations. Attempts to investigate effects of action on perception need to reverse this rather intuitive logic. Motor-visual priming paradigms attempt exactly this, by systematically manipulating response execution and subsequently measuring stimulus perception. The methodological difficulties arising from this reversal of the classical visual-motor paradigm are not trivial and, in some cases, can profoundly limit the conclusions drawn. Many of these problems arise from the inability to directly control participants response execution to the same extent that visual stimuli can be precisely controlled as independent variables. Measuring visual perceptual processing as a dependent variable is an equally difficult endeavour, as typically a motor response is required to index a participant's perception. Therefore, the only way to access effects of action on perception is to indirectly manipulate action parameters with task instructions and then indirectly measure perceptual processing. The methodological pitfalls associated with indirectly manipulating and measuring the variables of interest, as well as the measures taken to best avoid these pitfalls are described next.

1.1. The action cue

Manipulating a participant's state of action planning is typically achieved by an instruction to prepare a particular motor response, referred to as a 'cue', typically given at the beginning of an experimental trial. The prepared action is then either congruent or incongruent with a subsequently presented visual stimulus. Visual performance is then compared for congruent and incongruent stimuli and differences are interpreted as causal effects of planning a particular action on visual perception. The cue must be carefully controlled in order to avoid alternative interpretations of action-modulated vision.

Firstly, the cue should ideally instruct participants to prepare different actions randomly on a trial-by-trial basis. This is very often overlooked in motor-visual priming paradigms, with many studies manipulating the action cue across blocks, rather than individual trials. If the same cue is presented across all of the trials in an experimental block, participants have prior knowledge of the action before trial onset and can potentially pre-plan the movement. Any effects of action on perception observed under these circumstances may not necessarily reflect a temporally dynamic reallocation of perceptual resources to meet the current demands of an upcoming action. Instead, effects could reflect a shift in prioritising certain perceptual stimuli across an entire block of experimental trials. Ideally, the cue should randomly instruct one of a number of possible actions on each trial in order to avoid potential confounds of prior knowledge and/or pre-planning of the action type before trial onset. The experiments reported in this thesis manipulated cued responses randomly on a trial-by-trial basis to avoid this alternative interpretation.

Secondly, a direct match between the visual appearance of the response cue and the stimulus used to probe visual processing can be problematic. For example, imagine a task in which a leftward oriented arrow cues the preparation of a leftward reaching movement. During the preparation of the reaching movement, the same arrow stimulus is presented again, and participants must report the direction of the second arrow with a verbal response and subsequently execute the prepared reaching action. A compatibility effect may be observed in which congruent arrows have faster vocal response times than incongruent arrows. However, this effect may not be attributed to motor preparation given that the compatibility also exists at the level of the cue stimulus and the imperative stimulus. In other words, the stimulus may be primed by the visual appearance of the cue (i.e. stimulus-stimulus priming). Effects observed under these task conditions require additional control experiments to rule out the possibility of stimulus-stimulus priming (see Hommel & Müsseler, 2006, for an discussion of this issue). In the experiments reported here the cues did not visually match the perceptual stimulus in order to avoid alternative interpretations of stimulus-stimulus priming.

As well as avoiding a direct match between action cues and perceptual stimuli, ideally the cue stimuli should be arbitrarily mapped to responses in order to fully rule out instances of stimulus-stimulus priming. For example, participants can be instructed to prepare a response type (e.g. leftward/rightward grasp) according to the colour of a cue stimulus (i.e. blue/green) or according to the frequency of a tone (i.e. high/low). Under these circumstances the cue stimulus has no intrinsic relationship to the action type, but still evokes preparation of the action. This form of cue-response mapping also allows for counterbalancing the mapping across participants. However, an example of a non-arbitrary mapping would be leftward or rightward arrow stimuli that cue leftward and rightward grasping actions, respectively. Not only can this mapping not be counterbalanced, but any effect of priming (on a secondary perceptual stimulus) could be attributed not just to the planned grasping action, but to the feature intrinsic to the cue stimulus itself.

While arbitrary cue-response mappings may be optimal regarding the interpretation of results, when applied practically there are some notable disadvantages. Firstly, the arbitrary nature of the mapping is rather unintuitive for participants and therefore requires a greater number of practice trials, the use of feedback and/or regular reminders of the cue-response mapping between experimental blocks. Without taking any of these measures participants may readily forget the mapping and unknowingly prepare the wrong actions following the cue. Secondly, arbitrary cue-response mappings complicate the translation of the cue into a motor response, which likely requires additional cognitive processing time. This may add a further source of variance to the reaction times that a more intuitive non-arbitrary cue-response mapping may not.

Owing to the advantages and disadvantages of arbitrary cue-response mappings, across the tasks reported in this thesis a variety of different response cues were used that varied in their mapping to the instructed action. For example, in the experiments of Chapter 5, non-arbitrarily assigned visual cue-response pairs were used (i.e. letters 'R' and 'L' to instruct rightward and leftward grasping actions, respectively). In the experiment of Chapter 6, arbitrarily assigned and counterbalanced auditory cue-response pairs were used (e.g. high or low tone to instruct leftward or rightward grasping actions). In Chapters 3 and 4 arbitrarily assigned and counterbalanced visual cue-response pairs were used (e.g. blue or green fixation cross to instruct power or precision grasping actions). Importantly, where non-arbitrarily assigned cue-response mappings were used (Chapter 5: Exp. 1-3), care was taken to validate the interpretations made by using arbitrary cue-response mappings in a follow-up experiment (Chapter 6: Exp. 1).

1.2. Single vs. dual-task design

Tasks seeking to demonstrate effects of action on perception can have seemingly subtle differences in their task design that can influence the interpretation of their results. One of the most important distinctions is between single and dual task designs. Single tasks are variations on the classic GO/NOGO paradigm in which an initial cue stimulus (S1) instructs the preparation of a response (R1). The identity of a subsequently presented stimulus (S2) informs participants to either execute or withhold the prepared response. Importantly, R1 and S2 can be congruent such that they share a feature (e.g. right grasp orientation and right stimulus orientation) or incongruent such that they have opposing features (e.g. right grasp orientation and left stimulus orientation). The feature shared by the prepared action and the perceptual stimulus is usually task-irrelevant. Figure 1a illustrates the order of events for a prototypical experiment adopting a single task design. Under these task conditions, participants are preparing an action until the presentation of a (congruent or incongruent) GO-signal. Priming is observed when response times or accuracy differs between congruent and incongruent conditions. These differences are then interpreted as effects of action preparation on the perception of action-congruent stimuli.

However, the direction of effect in single tasks is not necessarily from action-to-perception, as many have pointed out (Miall et al., 2006; Vogt, Taylor, & Hopkins, 2003). It is conceivable that perceptual processing of the stimulus (S2) influenced the execution of the action (visual-motor priming), rather than the prepared action influencing perception of the stimulus (motor-visual priming). Indeed visual-motor priming has been observed many times (see Vogt & Thomaschke, 2007 for a review of visual-motor effects). Despite the ambiguity regarding the direction of effect, many studies have adopted single task designs. One approach to solving this ambiguity is to separate the prepared response from the perceptual response in a dual-task design.

In dual-task designs the cue stimulus (S1) instructs the preparation of a response (R1), but the execution of R1 is signalled by a neutral GO stimulus. During the preparation of R1 a second stimulus is presented (S2) which must be detected with an additional response (R2). Shared features between R1 and S2 results in a congruency between the two, even though

R1 and S2 now belong to functionally unrelated tasks. Under these task conditions, differences between congruent and incongruent trials in the reaction times or accuracy rates of R2 cannot be attributed to an effect of perceptual processing on potentiation of responses (visual-motor priming), as features of S2 cannot systematically influence R2. Figure 1b illustrates the order of events for a prototypical experiment with a dual task-design.

Although the direction of effects in dual-tasks is clearer than in single tasks, there are also some notable disadvantages to dual-tasks. Firstly, participants may adopt different strategies to overcome the apparent difficulty of completing two tasks simultaneously. For example, a participant may focus more of their effort on completing the 'motor' task, rather than the 'perceptual' task, or indeed the reverse. It is also conceivable that a participant may change their strategy throughout the task. It is very difficult to fully control for such strategic differences between or within participants. This inevitably represents a source of variance in the behavioural measures that is unknown in magnitude and unaccounted for. Single task designs do not suffer from this source of unwanted variance.

A second disadvantage of dual-tasks is the likely increased requirement for working memory resources compared to single tasks. Maintaining an action plan while simultaneously responding to a secondary stimulus could conceivably engage working memory resources to temporarily store the identity of the cue until after the GO-signal. This complicates the interpretations as an effect on perception may not necessarily reflect 'action planning', but instead an effect of encoding and/or maintaining the cue in working memory. Indeed the contents of working memory is known to influence visual perception (e.g. Olivers, Meijer, & Theeuwes, 2006). Although maintaining a representation of the cue in working memory may also occur during single tasks, dual-tasks may encourage this further. It is, however, reasonable to assume that the identity of the cue only needs to be encoded into working memory if it is removed from the display. Therefore, one way to discourage engagement of working memory processes is to present the cue throughout the entire delay until the onset of the imperative stimulus. This was done throughout all of the experiments reported in this thesis.

Like many behavioural investigations of effects of action on perception, both single and dual-task designs were adopted for the experiments reported in this thesis. Many of the aforementioned strengths and weaknesses of single and dual-task designs are not shared, so using a combination of both designs was deemed most appropriate. Care is taken to restrict the conclusions that can be confidently drawn from the findings where the experimental design limits the interpretations.

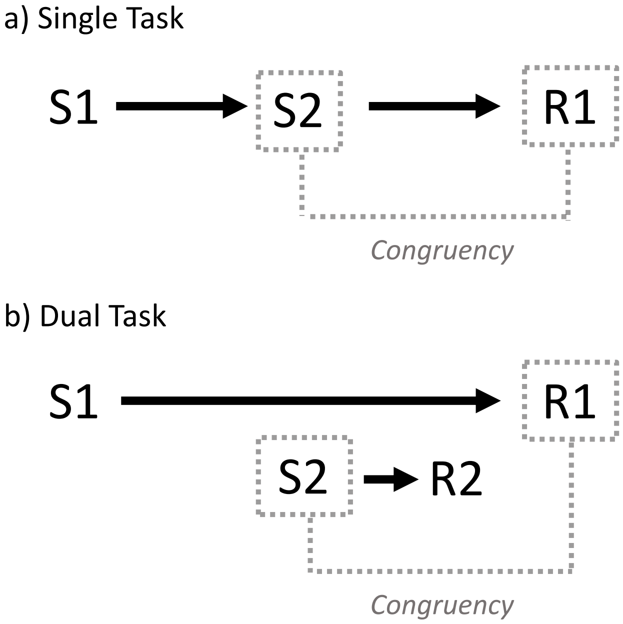

Figure 1. Diagram of single and dual-task motor visual priming paradigms. a) Single task designs first present a cue to prepare an action (S1), followed a perceptual stimulus (S2) which signals the execution of the prepared action (R1). b) Dual task designs first present a cue to prepare an action (S1), which is later signalled by a neutral GO-signal. Before the execution of the prepared action (R1) a perceptual stimulus is presented (S2) and responded to with a secondary response (R2). Action-perception congruency is defined by a task-irrelevant shared feature between S2 (perceptual stimulus) and R1 (the cued response). Diagram adapted from Thomaschke et al (2012).

2. Electroencephalography

In order investigate the mechanisms of action-modulated cognition, electroencephalography (EEG) was used in the experiments of Chapters 4 and 6. An overview of the neurophysiological basis of the EEG signal is provided next, followed by a detailed description of the processing and analysis choices made for the experiments reported in this thesis.

2.1. The EEG Signal

Cells in the brain communicate via a sequence of transient perturbations in their resting membrane potential, known as action potentials (APs). The sudden increase in the permeability of the cell membrane results in a positive spike in the voltage recorded in the cell. This change in potential propagates to the axon terminals where it triggers the release of neurotransmitters. These neurotransmitters then bind to the receptors of a post-synaptic neuron, resulting in a change in the permeability of the post-synaptic cell membrane, known as a post-synaptic potential (PSP). Unlike APs, which have a time course of approximately one millisecond, PSPs can span tens to hundreds of milliseconds. PSPs can also either be a positive change from resting membrane potential (excitatory) or a negative change from resting membrane potential (inhibitory). When large ensembles of cells fire simultaneously, a summation of PSPs takes place via the propagation of electrical fields in the surrounding tissues.

The scalp EEG signal originates not from action potentials, but predominately from the PSPs of large ensembles of cells that are both spatially aligned and receiving the same input (i.e. excitatory or inhibitory). Owing to these constraints, cortical pyramidal cells that lie perpendicular to the surface of the cortex are thought to contribute the majority of activity recorded in surface EEG (Coles & Rugg, 1995).

EEG therefore provides a direct, instantaneous and high-temporal resolution measure of neural activity. However, there are a number of caveats to the method that require consideration. Firstly, the EEG signal recorded at the surface of the scalp reflects only a portion of the entire neural activity present in the brain at any given time. Much of the activity arising from cortical cells that are not spatially aligned, fire asynchronously, receive different inputs (i.e. excitatory or inhibitory) as well as the activity of subcortical cells is largely inaccessible to this method. Secondly, owing to the spatial summation inherent to PSPs, the method suffers from low spatial resolution. Although scalp electrodes are commonly placed (and labelled) according to the underlying brain area they are supposedly recording from (see Figure 2), the signal at each electrode reflects the combined activity of an unknown number of neural sources (Luck, 2005). This is known as the *inverse problem* and imposes a limitation on the spatial specificity to which an effect can be attributed. While efforts are often made to estimate the source of scalp potentials, the precise origin of any given EEG signal measured at the scalp surface cannot be inferred to the same spatial specificity as other methods of brain imaging.

2.2. EEG acquisition

Modern EEG systems typically record from 32, 64 or 128 electrodes distributed according to a standard international 10-20 system (see Figure 2). The signal obtained from each electrode is the difference in voltage between an individual electrode and a common 'ground' electrode. The signal at each electrode is typically recorded relative to the average of two electrodes placed on the earlobes, the mastoids or a single electrode placed on the tip of the nose. These locations are used because they record much of the same ambient noise that is recorded by scalp electrodes, but crucially they record little to no neural activity. Subtracting the activity recorded from these external sites minimises the contribution of noise (e.g. from global voltage changes, surrounding electrical equipment or muscle activity). For all the recordings reported in this thesis, the earlobes were used.

The EEG data reported here were recorded continuously using a Biosemi ActiveTwo amplifier from 64 Ag-AgCl electrodes, placed according to the international 10-20 system (see Figure 2). Activity from horizontal eye movements was recorded from a pair of electrodes placed on the outer canthi of the eyes. Vertical eye movement activity was recorded from electrodes placed above and below the left eye.

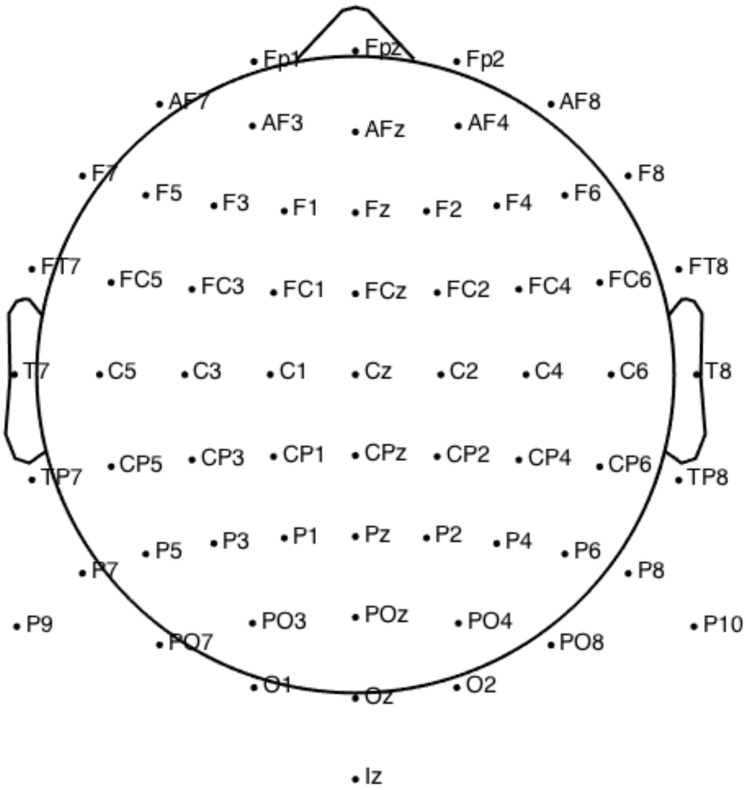

Figure 2. International 10-20 system of electrode positions.

3. Pre-processing EEG data

There are a number of important processing steps required before further analysis of the features of interest. Figure 3 outlines these pre-processing steps, which are discussed next in more detail.

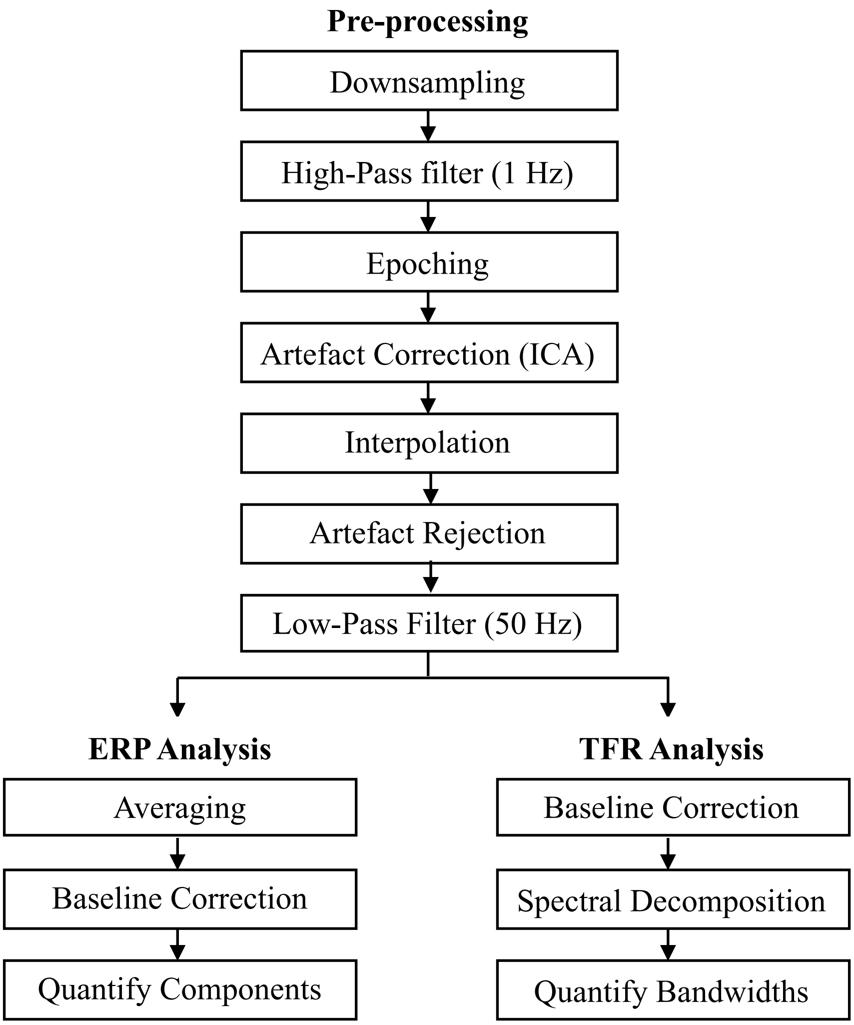

Figure 3. EEG data pre-processing and analysis pipeline

3.1. Downsampling

Higher sampling rates improve the temporal resolution of the EEG signal, although this improvement diminishes for sampling rates higher than approximately 500 Hz. The main advantage of downsampling is to save storage space and computational time needed to process the data. EEG data were recorded at a sampling rate of either 2048 Hz (Chapter 4) or 1024 Hz (Chapter 6) and subsequently downsampled to either 1024 Hz or 512 Hz, respectively.

3.2. Filtering

There are some well-known sources of noise in the EEG signal that are almost always expected to occur. In some cases, the noise is characterised by oscillations in the signal at a particular frequency. While preventing these sources of noise should always be encouraged before attempting to correct for them, in some cases filtering out certain frequencies is advantageous. For example, alternating current (AC) mains appliances have electromagnetic fields that induce a 50 Hz oscillation in the signal. Preventing this by using electrically shielded rooms and minimising AC appliances where possible can reduce this noise, however this is not always possible or practical. This presents a particular difficulty with investigating high frequency neural oscillations in the gamma band (30-150 Hz). However, when researchers are uninterested in frequencies beyond the beta band (13-30 Hz), it is common to apply a low-pass filter to remove frequencies above beta from the signal. Another filter is commonly applied to remove frequencies below approximately 1 Hz. This is because relatively slow changes in the potentials measured at the scalp (below 1 Hz) are thought to reflect changes in conductance from sweating rather than neural activity.

Filtering EEG data will inevitably distort the signal and should only be applied where appropriate. Deciding on appropriate filtering requires a balance between removing as much noise as possible while minimising distortions of the signal. Filtering out very high (> 50 Hz) and very low (< 1 Hz) frequencies should not substantially distort the signal, so data in the current experiments were first high-pass filtered at 1 Hz and subsequently low-pass filtered at 50 Hz.

3.3. Epoching

The continuous EEG signal is divided into intervals of data time-locked to an event of interest. These intervals are known as epochs, which are later averaged together or can analysed individually in single-trial analyses. The length of the epochs to be extracted will depend on the researcher's hypotheses as well as the type of analysis to be performed on the epochs. However, extracting unnecessarily long epochs can increase the likelihood of including noise in the epochs. This will then increase the likelihood of unnecessarily rejecting more epochs from an analysis in the subsequent step of artefact rejection. In the experiments reported here, epochs for ERP analysis are extracted that begin just before the presentation of the visual stimuli of interest (e.g. -100ms relative to stimulus onset) and end after the stimulus onset (e.g. +600ms relative to stimulus onset). Epoch length for time-frequency analysis is typically longer (e.g. -300ms to +1000ms relative to stimulus onset). Longer epochs are typically extracted for time-frequency analysis because of a decrease in temporal precision that is inherent to time-frequency analysis (see section Time-Frequency Analysis for more details).

3.4. Artefact correction (Independent Component Analysis)

Ocular activity including eye-movements and blinks cause large distortions in the EEG signal, particularly at frontal electrode sites. Participants may also repeatedly make eye-movements or blinks at the same time points across trials, for example following the sudden onset of visual stimulus. Sources of noise that are non-randomly distributed across trials can significantly distort ERP waveforms. Instructing participants to minimise their eye-movements and blinks is essential, however these sources of noise are necessarily unavoidable. Eye-movements and blinks generate very distinctive profiles of activity in the EEG signal, which makes it possible to identify and correct for them using a signal processing method known as Independent Component Analysis (ICA).

ICA attempts to decompose a multivariate signal into maximally independent subcomponents. The method is a spatial filter used to decompose the EEG signal into a number of constituent subcomponents, or theoretical sources. Some of these components will represent the signal likely to be caused by eye-movements and blinks. Components generated by ocular activity are relatively distinctive due to their frontal distribution and smoothly decreasing frequency responses. In order to 'correct' for ocular artefacts, all of the components can be computed back into the EEG waveform, minus those identified as eye-movement and blink related. The primary advantage of this method of artefact correction is to recover data that would otherwise need to be rejected.

In the experiments reported here ICA was used to correct for eye-movement and blink artefacts. In order to improve the identification of horizontal eye-movements, additional electrodes are placed on the outer canthi of the eyes, and for blinks above and below the left eye.

3.5. Interpolation

It is possible that the data from an electrode can be missing entirely, either due to damage or such a poor connection that the signal is irreparably noisy. Under these circumstances it is common to reconstruct the missing signal by interpolating the signal using nearby electrodes. A common method of interpolation is known as spherical linear interpolation, which was adopted for the experiments reported in this thesis.

3.6. Artefact rejection

A certain portion of trials will inevitably contain signal that may not be generated from a neural source. Some of this signal can be assumed to be noise, due to the known properties of the brains neurophysiology. For example, very abrupt fluctuations in the amplitude of the signal (±100 µV) cannot be caused by neural activity. These fluctuations are most likely caused by a momentary loss of adequate connection, from movement artefacts, or intermittently faulty electrodes. It is therefore common to exclude trials from further analysis that contain voltage steps exceeding ± 100 µV, which was adopted for the experiments reported in this thesis.

4. Event-Related Potential Analysis

4.1. Baseline correction

ERP waveforms should be normalised relative to a baseline signal. On any given trial the amplitude of a waveform may shift or offset. To remedy this, the mean amplitude in a pre-stimulus interval (e.g. -200ms to 0ms relative to stimulus onset) is subtracted from amplitudes at the remaining time points after stimulus onset. The length of the pre-stimulus interval used for baseline correction will influence how representative the baseline measure will be. Although there is no consensus on how long this should be, it is generally accepted that intervals below 100ms are sub-optimal (Luck, 2005). Baseline corrections for the experiments reported here were made using the pre-stimulus interval from -100ms to 0ms.

4.2. The ERP Component

After averaging across trials and normalising the ERP waveform to a baseline, the resulting waveform consists of several positive and negative deflections, referred to as components. Luck (2014, p. 69) provides a concise definition of ERP components as follows.

> "An ERP component can be operationally defined as a set of voltage changes that are consistent with a single neural generator site and that systematically vary in amplitude across conditions, time, individuals and so forth. That is, an ERP component is a source of systematic and reliable variability in an ERP data set."

The ERP components of interest in this thesis are visual sensory responses, in particular early visually evoked components. The typical visually-evoked potential contains a number of components demarcated both by their polarity (see section on C1 below for an exception to this) and order (i.e. the P1 component refers to the first positive component).

4.3. C1

The first component observed following a visual stimulus is the C1 component, which onsets between 40 and 60ms post-stimulus and peaks between 80 and 100ms post-stimulus at midline posterior electrode sites. The component is not labelled with a 'P' or 'N' because its polarity can vary, for example it can be positive or negative depending on the presentation of the visual stimulus in the lower or upper visual fields, respectively (Clark, Fan, & Hillyard, 1994; Jeffreys & Axford, 1972). Together with this retinotopic mapping, strong converging evidence supports the neural source of the C1 component as primary visual cortex near the location of the calcarine fissure (Clark et al., 1994; Di Russo, Martínez, Sereno, Pitzalis, & Hillyard, 2002). However, unless stimuli are presented in the upper visual field, the (positive) C1 wave typically sums together with the subsequent positive component (P1) into a single positive wave.

4.4. P1

The P1 onsets between 60 and 90ms post-stimulus, peaking between 100 and 130ms post-stimulus at lateral occipital sites. The likely origin of the P1 wave is the extrastriate visual cortex (Di Russo et al., 2002). Some evidence also suggests that the P1 contains two subwaves, an early wave peaking around 75ms post-stimulus and a later wave peaking around 100ms post-stimulus (Clark et al., 1994). Combined ERP dipole modelling and fMRI have localised the earlier portion of the P1 component to dorsal extrastriate cortex (middle occipital gyrus), and the later portion more ventrally from the fusiform gyrus (Di Russo et al., 2002).

4.5. N1

Similarly to the P1 component, the N1 is thought to be composed of a number of subcomponents that sum together to form the N1 peak. The first peaks between 150 and 200ms post-stimulus at anterior electrode sites, followed by two posterior subcomponents peaking between 150 and 200ms post-stimulus at parietal and lateral occipital sites. The earliest anterior component can be localised to the superior parietal cortex, close the intraparietal sulcus (Di Russo et al., 2002), while the later posterior components can be localised to the same sources as the P1 component.

While all three of these N1 subcomponents are largely unaffected by stimulus location, they are all influenced by spatial attention such that stimuli elicit larger N1 amplitudes when the location at which they are presented is attended, compared to unattended (Hillyard & Anllo-Vento, 1998; Mangun, 1995).

4.6. Quantifying ERP components

In order to compare ERP components across experimental conditions, an accurate measure of the size of an ERP component is required. Components can be quantified in a number of different ways, which can strongly influence the outcome of a comparison. Some of the most common methods of quantifying the size (or amplitude) of ERP components are now discussed.

The simplest and oldest measure is the *peak amplitude*, which is computed as the maximum (or minimum) voltage occurring within a pre-defined time interval. For example, the peak amplitude of the first positive component of a visual evoked potential (termed the P1 component) can be extracted as the maximum voltage occurring between approximately 70ms to 110ms post stimulus onset. However, because peak amplitude measures reflect the voltage at just one time point, they are particularly vulnerable to distortion from noise in the data. This is even more problematic when comparing ERP waveforms derived from different trial numbers, as the peak amplitude will systematically increase with decreasing trial numbers. Ideally ERP waveforms would reflect the average from the same number of trials across conditions, however trials may be rejected for a number of reasons (e.g. containing noise artefacts or behavioural errors) often resulting in uneven trial numbers.

A superior approach is to compute the *mean amplitude,* which is the average voltage at all time points within an interval. This measure is not only less vulnerable to systematic distortions from varying trial numbers compared to peak measures, but also better appreciates the ERP component as a phenomenon that is extended over time. However, the mean amplitude measure remains vulnerable to baseline differences that may exist between experimental conditions. In this case it can be advantageous to calculate the *mean peak-to-peak* measure of a component, which is the difference between two mean amplitude components. For example, the difference between the mean P1 and N1 values can reflect the magnitude of the N1 component, irrespective of baseline differences.

It should be noted that all of the aforementioned measures suffer from the problem of how to define the measurement interval, albeit to varying degrees. While mean amplitude measures may be superior to peak amplitude measures, they remain sensitive to the length and position of the time interval used to calculate them. There is no simple way to overcome this limitation, however previous research is often used to guide decisions of measurement intervals. For example, the mean amplitude of the P1 component is often measured in a 40ms interval approximately 70ms to 110ms after the onset of a visual stimulus. However, using previous research to guide choices of measurement intervals is not always straightforward. For example the luminance of a visual stimulus is known to shorten the latency of the P1 component, so an experiment with brighter stimuli may require a shift in the interval to optimally measure the component (Luck, 2014). Similarly, visual stimuli presented in the lower visual field will generate a positive C1 component that sums together with the P1 component, shifting the apparent P1 latency in time.

4.7. *Using ERPs to measure covert processes*

ERP measurement can complement behavioural investigations by providing a means of covertly measuring a cognitive process, when a behavioural response is problematic in a design. For example, recording ERPs from infants, who cannot be instructed to respond in a particular way, can nevertheless provide a covert measurement of cognitive processing.

The ERP methodology has been extensively used to covertly measure visuo-spatial attentional processing. The underlying logic is that stimuli falling within an attended area of space receive enhanced processing, regardless of the stimuli's task relevance (Heinze et al., 1994). Therefore enhanced ERP components are observed in response to task-irrelevant visual 'probe' stimuli presented in an attended area relative to an unattended area of space (Hillyard, Vogel, & Luck, 1998; Hillyard & Anllo-Vento, 1998). Further data suggest that the early P1/N1 components also reflect a biasing mechanism operating on processing of non-spatial features (Karayanidis & Michie, 1997; Valdes-Sosa et al., 1998; Zhang & Luck, 2009), consistent with object based attentional selection at early stages of visual processing. This method is adopted in Chapter 4 to investigate early sensory processing of object size during the preparation of power and precision grasping actions.

5. Time-Frequency Analysis

The EEG signal contains rhythmic activity reflecting fluctuations in the excitability of large populations of neurons. When large ensembles of neurons are synchronously active, the sum of the neurons' electrical fields become large enough to be recorded from the scalp sensors.

5.1. Spectral decomposition

The rhythmic signal obtained from the scalp sensors contains multiple different frequencies simultaneously, which can be decomposed through signal processing techniques. These frequencies are grouped into bands including delta (2-4 Hz), theta (4-8 Hz), alpha (8-12 Hz), beta (13-30 Hz) and gamma (30-150 Hz). While there are no precise boundaries between individual frequency bands, the broad boundaries are defined by neurobiological mechanisms of synaptic decay and signal transmission dynamics (for more information see Buzsáki, 2006; Buzsáki & Draughn, 2004).

There are many ways to obtain frequency estimates from EEG data. Most of these methods rely on the mathematical procedure of *convolution*, which can be thought of as one signal weighted by another signal that slides along the first signal in time. It is then possible to compute what the first signal and the second signal have in common, over time. The frequency content of the second signal can be carefully controlled in order to estimate the approximate frequency content of the first signal (i.e. an EEG signal). To do this a time-series limited sinusoidal wave (known as a wavelet) is repeatedly convolved with an EEG signal over time to reveal approximately when the EEG signal contains data similar to the frequency limited wavelet. The resulting data are referred to as a Time-Frequency Representation (TFR) of the EEG data. The utility of TFR analysis is to isolate frequency-band-specific activity over time. A discussion of the many techniques of obtaining TFR data is beyond the scope of this thesis, so the reader is referred to Cohen (2014) and Roach and Mathalon (2008) for detailed discussions of the topic.

Regardless of the technique used for spectral decomposition of EEG data, virtually all methods balance a compromise in temporal and frequency resolution. This is because time-frequency decomposition in general relies on estimating the spectral content at a given time point based on a combination of the spectral content at neighbouring time points. This means that the larger the 'window' used to estimate the frequency content at a given time point, the greater the frequency resolution but the poorer the temporal resolution. The method of time-frequency decomposition used in this thesis is known as *complex* Morlet wavelet analysis, which uses wavelets consisting of multiple sinusoidal waves with Gaussian tapers. This is one of the most common methods of time-frequency decomposition and is known to be well suited to localising frequency information in time for EEG data (Cohen, 2014).

5.2. Sensorimotor beta rhythm

Cued motor preparation is accompanied by prominent changes in the power of beta oscillations (13-30Hz) over central electrode sites (Cheyne, 2013; Kilavik, Zaepffel, Brovelli, MacKay, & Riehle, 2013; Pfurtscheller, Stancák, & Neuper, 1996b). The source of these power changes is commonly attributed to the contralateral pre-Rolandic 'sensorimotor' region (Pfurtscheller & Berghold, 1989). While the exact functional role of beta band activity in cued movement tasks is not yet clear (Kilavik et al., 2013), there is a general consensus that beta band oscillations provide a reliable indicator of the onset of movement preparation, execution as well as motor imagery (Kuhn et al., 2006; Pfurtscheller & Lopes da Silva, 1999; Pfurtscheller & Neuper, 1997) and may reflect an active process promoting existing motor or cognitive states (Engel & Fries, 2010).

Studies typically report event-related *desynchrony* (ERD) in the hemisphere contralateral to the hand used to execute the movement and event-related *synchrony* (ERS) in the hemisphere ipsilateral to the hand used (Taniguchi et al., 2000). ERS is observed when the behaviour of large numbers of neurons synchronises (Pfurtscheller, Stancák, & Neuper, 1996a) and most likely requires coherent activity of cell assembles over at least several square centimetres (Lopes da Silva, 1991). Initially, beta ERS was thought to reflect the activation state of the sensorimotor system with ERS reflecting an 'idle' state and ERD an activation state (Pfurtscheller et al., 1996b). This idea was supported by combined EEG/fMRI studies linking ERD to cerebral activation (Formaggio et al., 2008; Stevenson, Brookes, & Morris, 2011; Yuan et al., 2010). However more recent theories suggest that ERS instead reflects a maintenance of the current sensorimotor or cognitive state (Engel & Fries, 2010; cf. Jenkinson & Brown, 2011), or even the dynamics of decision making processes (Spitzer & Haegens, 2017).

Chapter 3: MOTOR PREPARATION AND THE PRIMING OF LOCAL/GLOBAL STIMULUS FEATURES[1]

1. Abstract

Preparing simple actions can facilitate reaction times to stimuli that contain an action-relevant perceptual feature. Previous research has shown that stimuli are responded to faster if they are located at the goal location of an upcoming reaching action, are orientated in the same direction as a grasping action, or if their size matches the aperture of a grasping action. This influence of action on perception is assumed to reflect mechanisms of selection in visual perception tuned to current action goals, such that action relevant sensory information is prioritized relative to less relevant information. Beyond stimulus features such as location, orientation and size, the hierarchical structure of visual stimuli (the local elements and the global whole) may also be an action relevant perceptual feature. In two experiments, the influence of preparing a movement (power vs. precision grasping actions) on the processing of hierarchical stimulus information (local vs. global target detection) was investigated. Local targets were detected faster following precision, relative to power grasp cues. The results suggest that the hierarchical dimension of objects may be a relevant perceptual feature for grasp programming. To our knowledge, this is the first evidence that preparing different magnitudes of the same basic action has systematic effects on visual processing of the hierarchical structure of objects.

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[1] The findings from this chapter are published in *Cortex* (Job, van Velzen, & de Fockert, 2017)

2. Introduction

The ways in which perception can influence action have been widely investigated (for a review see Vogt & Thomaschke, 2007), however much less is known about how exactly the planning of simple actions can modulate ongoing visual perception. Much of the evidence for effects of action on perception comes from motor-visual priming paradigms, which investigate perceptual processing of stimuli that contain features relevant to a planned action and have revealed that perception can indeed be biased toward action relevant features. Early behavioural experiments (Craighero, Fadiga, Rizzolatti, & Umilta, 1999) demonstrated that a visual stimulus is detected faster if it has the same orientation as a prepared grasping action. Subsequent evidence for motor-visual priming has compared grasping and pointing movements and demonstrated that the processing of object size is selectively enhanced during grasp preparation (Fagioli et al., 2007) as well as processing of object orientation (Bekkering & Neggers, 2002; Gutteling et al., 2011; Hannus, Cornelissen, Lindemann, & Bekkering, 2005). These findings suggest that action preparation may tune incoming sensory information to the perceptual features relevant for the upcoming action, resulting in a bias in visual processing to match the prepared action.

A number of findings suggest that the hierarchical structure of stimuli may be influenced by grasp preparation. For example Vainio and colleagues (2006) found an object affordance size effect (size of task-irrelevant objects influences power/precision grasp responses), however the effect only occurred when holding a precision device in the right hand and the power device in the left hand. In a further study (Vainio et al., 2007), right hand responses to the ‘local’ component of an object (e.g. the stalk of a fruit) were facilitated when it was part of a precision-graspable ‘global’ object (e.g. a strawberry) while left hand responses to the same object were facilitated when it was part of a power-graspable object (e.g. an apple). These findings suggest that object information pertaining to power and precision grasping is predominantly processed in the right and left hemispheres, respectively, and that the processing of hierarchical structure of objects is linked to power/precision grasping actions. More recently Gable, Poole and Cook (2013) also used unilateral hand contractions to activate the right or left central parietal hemispheres and observed behavioural facilitation of global and local processing, respectively. Performance on tasks of local and global processing is also influenced when stimuli are presented near to the hands (Davoli et al., 2012; Langerak et al., 2013; Thomas, 2015), effects often interpreted as a facilitation of perceptual information relevant to covert manual action preparation (Gozli et al., 2012; Makin et al., 2012; Reed et al., 2010).

Additionally, evidence from a variety of approaches suggests that both precision/power grasping and local/global processing may share a similar pattern of hemispheric lateralization. Findings have long supported the notion that the local and global levels of hierarchical stimuli are predominantly processed in the left and right hemispheres, respectively. Behavioural (Hübner, 1998; Van Kleeck, 1989) as well as imaging studies using PET (Fink et al., 1998), fMRI (Fink et al., 1996, 1997) and electrophysiology (Evans et al., 2000; Malinowski et al., 2002) support the lateralization of global (right hemisphere) and local (left hemisphere) processing. Some causal evidence is provided from neuropsychological studies of patients with left/right temporal-parietal lesions exhibiting selective impairment in local/global stimulus processing (Robertson & Lamb, 1991; Robertson, Lamb, & Knight, 1988). In healthy subjects, causal evidence for an asymmetry was provided by Romei and colleagues (2012) who impaired global processing with right-parietal rTMS and local processing with left-parietal rTMS. However, some inconsistencies exist within the neuropsychological literature, as a common feature of Bálint's syndrome is simultanagnosia, a selective impairment in global stimulus processing with intact local processing, which results from *bilateral* damage to parieto-occipital junction (Farah, 1990),

In the current chapter, motor-visual priming of local/global stimulus features was investigated in two experiments. In Experiment 1, participants were required to detect a target stimulus presented at the local or global level of a compound stimulus following a cue to prepare either a power or precision grasp. If the magnitude of grasp preparation biases visual processing toward stimulus features relevant for the upcoming action, then detection of local targets should be facilitated during the preparation of precision grasping relative to power grasping, and detection of global targets should be facilitated during power grasping, relative to precision grasping. Experiment 2 sought to replicate findings from Experiment 1 while also reducing the number of local elements within the compound stimuli, a manipulation known to reduce the commonly observed global bias in tasks using hierarchical stimuli (Kimchi, 1988; Martin, 1979; Yovel, Yovel, & Levy, 2001). This was done in order to investigate whether effects of action preparation on local/global processing are dependent on the commonly observed global bias in visual processing. Three pilot studies are also reported in the Appendix. In these pilot studies, the paradigm was refined by investigating whether simply executing the power/precision grasping actions either concurrently (Pilot 1), or non-concurrently in a separate grasping task (Pilot 2) was sufficient to bias local/global processing. Additionally, the influence of preparing either a grasping versus pointing action on local/global processing was investigated (Pilot 3). The results of these pilot studies suggested that simply executing grasping actions is not sufficient to induce a biasing of local/global stimulus features, although local/global processing may be influenced during the planning phase of a grasping movement (see the

Appendix for more details). These pilot studies therefore led to the implementation of the motor-visual priming paradigms reported next.

3. Experiment 1

3.1. Participants

A total of 16 participants (13 female) with a mean age of 21 years (SD = 4.02) participated in return for course credits or £10. All participants were right handed (mean laterality quotient (Veale, 2014) = 92.21, SD = 11.06) and reported normal or corrected to normal vision. The Local Ethics Committee at Goldsmiths, University of London, approved all experimental protocols and the experiment adhered to the ethical guidelines presented in the 1964 declaration of Helsinki. All participants provided written informed consent before the beginning of each experiment and were debriefed at the end of the experiment as appropriate.

3.2. Stimuli and Task

A local/global target detection task run with E-prime software (Schneider, Eschman, & Zuccolotto, 2002) required participants to respond when presented with a target shape stimulus. The target shape could appear at either the local or the global dimension of a compound stimulus (target present trials) or the stimulus could be comprised only of non-target shapes (target absent trials). Compound stimuli were composed of 13-20 local shapes (squares, circles or crosses) (0.76° visual angle) arranged into a global configuration (square, circle or cross) (3.8° visual angle). All shape combinations at the local and global dimensions were presented, excluding same-shape combinations (e.g. a global square comprised of local squares).

On each trial, before target presentation, a coloured fixation cross (.91° visual angle) instructed participants to prepare either a power or a precision grasp (see Figure 4 and Figure 5 for schematics of the response devices and trial procedure, respectively). At 1000ms following the grasp cue a compound stimulus was presented for 250ms. Participants were instructed to execute the prepared grasp as fast as possible if a pre-specified target shape (square) was present at either the local or the global dimension and to withhold the grasp in the absence of the target shape. A black fixation cross was presented during the inter-trial interval for either 800ms, 900ms or 1000ms, randomly.

3.3. Procedure

Following provision of written consent and the revised Edinburgh Handedness Inventory (Veale, 2014), participants completed a practice block of 20 randomised trials, followed by six blocks of 60 randomised trials with self-timed breaks between blocks. At the start of each block participants received an instruction on the screen to hold the devices in either their left or right hand. The instruction alternated such that half of the trials were completed with the left hand and half with the right hand. A power or precision grasp cue was presented on each trial with equal probability. The hierarchical stimulus presented on each trial contained a target at the global level, the local level or at neither level with equal probability (120 trials each). Therefore, each of the eight possible conditions (power/precision cue with the left/right hand followed by a local/global target) consisted of 30 trials. The entire session lasted approximately 25 minutes. The mapping between the colour of the cue (blue/green) and the grasp (power/precision) was counterbalanced across participants. The hand used to execute the grasps was also counterbalanced such that half of participants used their right hand for even numbered blocks and their left hand for odd numbered blocks while the reverse was true for the remaining half of participants.

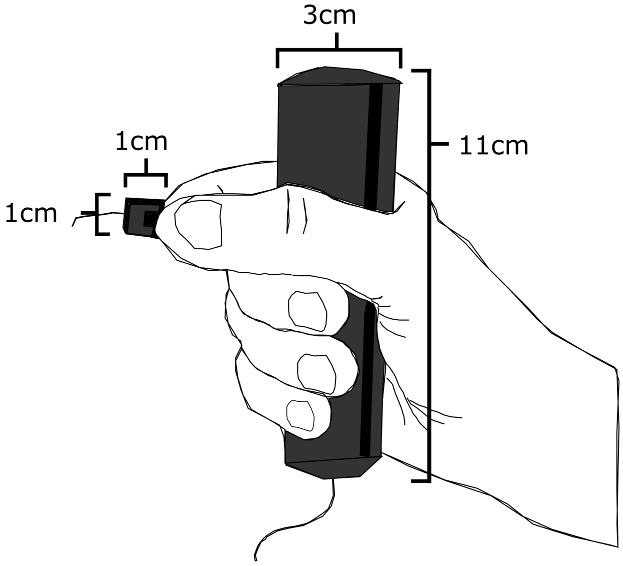

Figure 4. Schematic illustration of power and precision response devices. Precision grasps required pressing the small button with the thumb and the opposing index finger, while power grasps required pressing the large cylindrical device with the whole palmar surface of the hand.

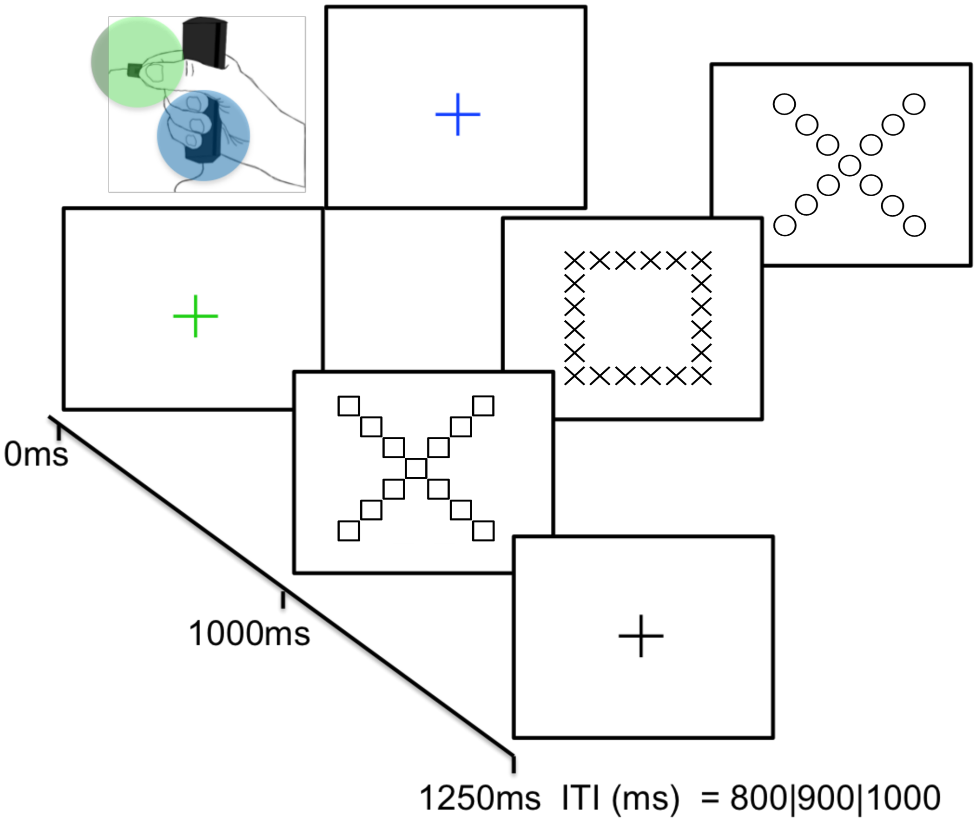

Figure 5. Trial procedure for Chapter 3: Experiment 1.
Following the coloured precision or power grasp cue (0ms) a compound stimulus was presented for 250ms that could contain a target shape (e.g. square) at the local or global level, in which case participants executed the cued grasp. If the target was absent, the prepared grasp had to be withheld. The inter-trial interval (ITI) was randomly varied to be 800ms, 900ms or 1000ms. Images are not to scale.

3.4. Results

Reaction times in response to local and global targets were compared using a 2x2x2 repeated measures Analysis of Variance (ANOVA) with factors of target level (local/global), grasp (power/precision) and hand (left/right). Table 1 shows the mean percentage errors made across conditions. As errors were made on an average of only 3.5% of trials, they were not further analysed and only trials in which a correct response was recorded were included in the reaction time analysis.

Table 1. Error rates (%) with standard deviations for Experiment 1 & 2 Chapter 3.

	Global Target		Local Target	
	Power	**Precision**	**Power**	**Precision**
Experiment 1	3.04 (2.59)	3.56 (3.69)	4.08 (3.91)	3.21 (3.85)
Experiment 2	3.56 (3.13)	4.86 (3.48)	3.82 (4.52)	2.69 (2.51)

Figure 6 shows the mean reaction times to global and local targets using power and precision grasps with the left (a) and right (b) hand. A main effect of grasp magnitude was observed with faster execution of precision grasps (M = 421, SD = 79.06) than power grasps (M = 439, SD = 88.94) by 18ms (SE = 6.73), *F*(1, 15)= 7.32, p = .016, η_P^2 = .328. A main effect of target level was also observed with faster responses for global (M = 418, SD = 85.59), compared to local targets (M = 442, SD = 82.42) by 24ms (SE = 5.18), *F*(1, 15)= 22.74, p < .001, η_P^2 = .603. There was no main effect of the hand used, *F*(1, 15)= .58, p = 456, η_P^2 = .048 or interactions involving the factor of hand.

An interaction between grasp magnitude and target level was observed (*F*(1, 15)= 6.40, p = .023, η_P^2 = .299) indicating that the cued grasp magnitude influenced reaction times to local and global targets. Post-hoc t-tests confirmed that responses to local targets were faster using precision grasps (M = 427, SD = 72.68) compared to power grasps (M = 456, SD = 87.32) by 29ms (SEM = 7.99), t(15) = 3.63, p = .002. The effect of grasp was not significant for global targets (t(15) = .93, p = .365).

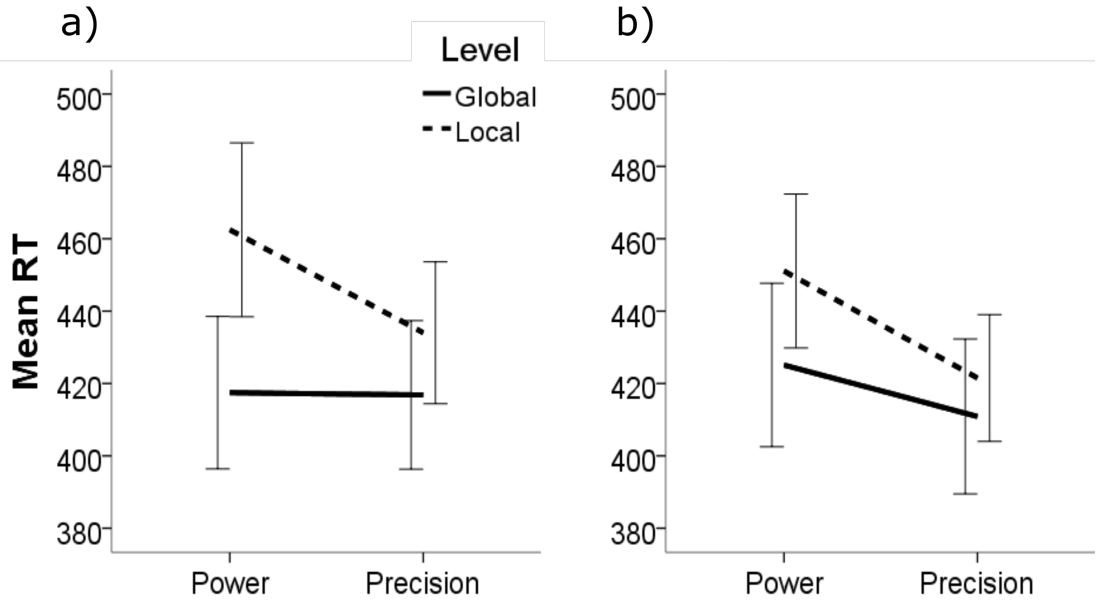

Figure 6. Mean reaction times (ms) for Chapter 3: Experiment 1**.**
Mean reaction times (RT) in milliseconds to target stimuli presented at the global and local levels of a compound stimulus, separated for power and precision grasping. Responses are made with either the left hand (a) or the right hand (b). Error bars represent +/- 1 SE.

3.5. Discussion

The results of Experiment 1 show that the preparation of either a precision or power grasp can selectively modulate the processing local visual information. Local level targets were detected faster following preparation of a precision grasp, relative to a power grasp. This finding suggests that variation in the same basic action (a grasp) can selectively influence detection of a subsequent visual local target. In contrast to previous evidence suggesting a hemispheric asymmetry for power and precision grasping (Vainio et al., 2006, 2007) the hand used to execute the movements had no influence on power/precision response times in Experiment 1.

The effect of the prepared grasp was only present in terms of detection of local targets, whereas global target detection was unaffected by grasp preparation. A possible factor contributing to this asymmetry is that we used compound stimuli that consisted of a relatively large number of densely organized local elements. Previous work has shown that the magnitude of global bias is dependent on stimulus features such as size and density (Kimchi, 1988; Martin, 1979; Yovel et al., 2001). For example displays with densely arranged local elements spaced close together promote a strong global precedence (Caparos, Linnell, Bremner, de Fockert, & Davidoff, 2013; Enns & Kingstone, 1995; Martin, 1979), meaning that global target detection is greatly facilitated relative to local target detection. In the current study, responses were indeed substantially faster to global, compared to local, targets, which may have obscured any subtle effects of grasp preparation on detection of global targets. Experiment 2 was therefore run in order to replicate the findings of Experiment 1 and to investigate the effects of action preparation on detection of local and global targets in displays in which the global level of the compound stimulus was made less salient by using fewer and less densely organized local elements.

4. Experiment 2

4.1. Participants

A total of 16 adults (12 female) with a mean age of 24 years (SD = 4.83) participated in return for £10. All participants were right handed (mean laterality quotient (Veale, 2014) = 87.5, SD = 23), and reported normal or corrected to normal vision. The Local Ethics Committee at Goldsmiths, University of London, approved all experimental protocols and the experiment adhered to the ethical guidelines presented in the 1964 declaration of Helsinki. All participants provided written informed consent before the beginning of each experiment and were debriefed at the end of the experiment as appropriate.

4.2. Stimuli and Task

The task was identical to Experiment 1, except the compound stimuli consisted of fewer local shapes (9-12) spaced further apart (see Figure 7). This manipulation of the saliency of the global level has been previously successfully used in order to reduce the relative saliency of the global level (Caparos et al., 2013).

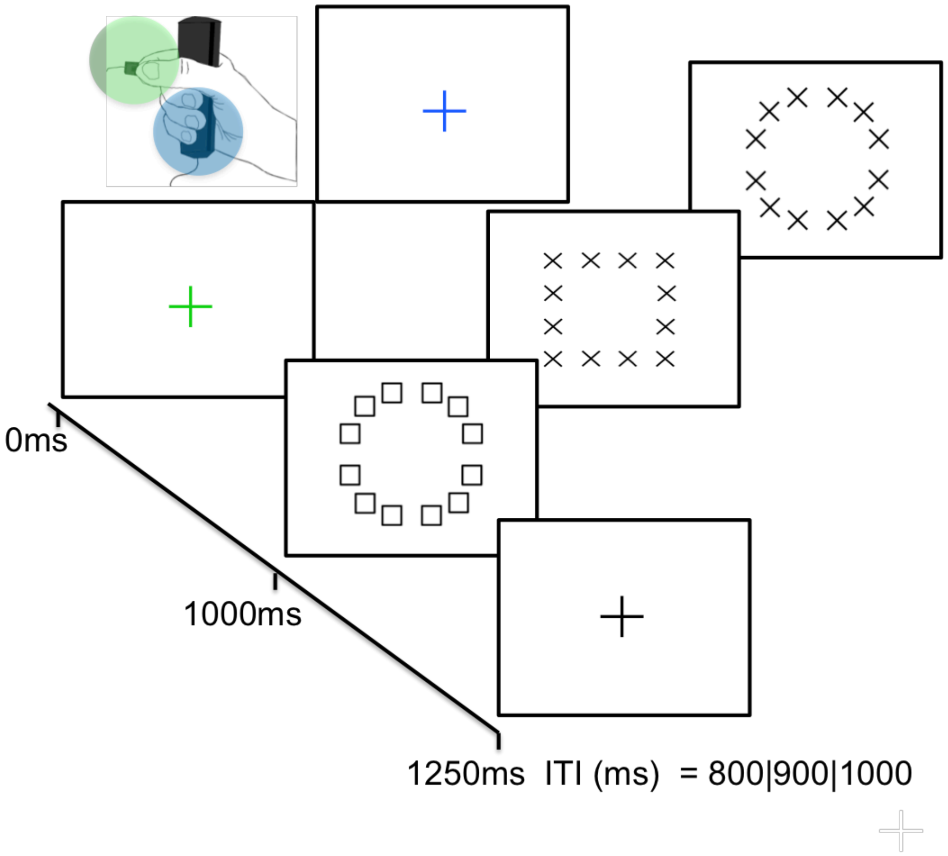

Figure 7. Trial procedure for Chapter 3: Experiment 2.
Schematic illustration of the trial procedure with alternate possibilities superimposed above. Following the coloured precision or power grasp cue (0ms) a compound stimulus was presented for 250ms that could contain a target shape (square) at the local or global level, in which case participants executed the cued grasp. If the target was absent, the prepared grasp had to be withheld. The inter-trial interval (ITI) was randomly varied to be 800ms, 900ms or 1000ms. Images are not to scale.

4.3. Results

Errors were made on an average of only 2.9% of trials, so were not further analysed. Reaction times were analysed using the same 2 (target level: local vs. global) x 2 (grasp: power vs. precision) x 2 (hand: left vs. right) ANOVA as Experiment 1.

Figure 8 shows the mean reaction times to global and local targets using power and precision grasps with the left (a) and right (b) hand. A main effect of grasp magnitude was observed with faster precision responses (M = 468, SD = 83.68) compared to power (M = 489, SD = 83.25) by 21ms (SE = 5.37), $F(1, 15) = 15.82$, p = .001, $\eta_p^2 = .513$. No main effect of target level (*F*(1, 15) = .838, p = .374, η_P^2 = .053) or hand (*F*(1, 15) = .008, p = .931, η_P^2 = .001) was found.

A marginally significant interaction between the target level (local/global), the grasp magnitude (power/precision) and the hand used (left/right) was observed, *F*(1, 15) = 4.56, p = .050, η_P^2 = .233. To investigate this interaction further, separate two-way ANOVAs with factors of level (local/global) and grasp magnitude (power/precision) for each hand confirmed a significant interaction between level and grasp, *F*(1, 15) = 7.97, p = .013, η_P^2 = .347 for right hand responses. Post-hoc t-tests revealed that right hand responses to local targets were faster using precision (M = 460, SD = 68.61) relative to power (M = 498, SD = 79.85) grasps by 38ms (SEM = 9.21), t(15) = 4.09, p = .001. This difference was not significant for left hand responses to global targets, t(15) = -.42, p = .684. The two-way interaction between target level and grasp magnitude was not significant for left hand responses, *F*(1, 15) = .409, p = .532, η_P^2 = .027[2].

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[2] The possibility that detection of this effect was precluded by low statistical power, as a result of an inadequate sample size, is unlikely as given the sample effect size of Experiment 1 and a critical threshold of .05 (two-tailed), a minimum of 12 participants was required for Experiment 2 with .80 statistical power to reject the null hypothesis.

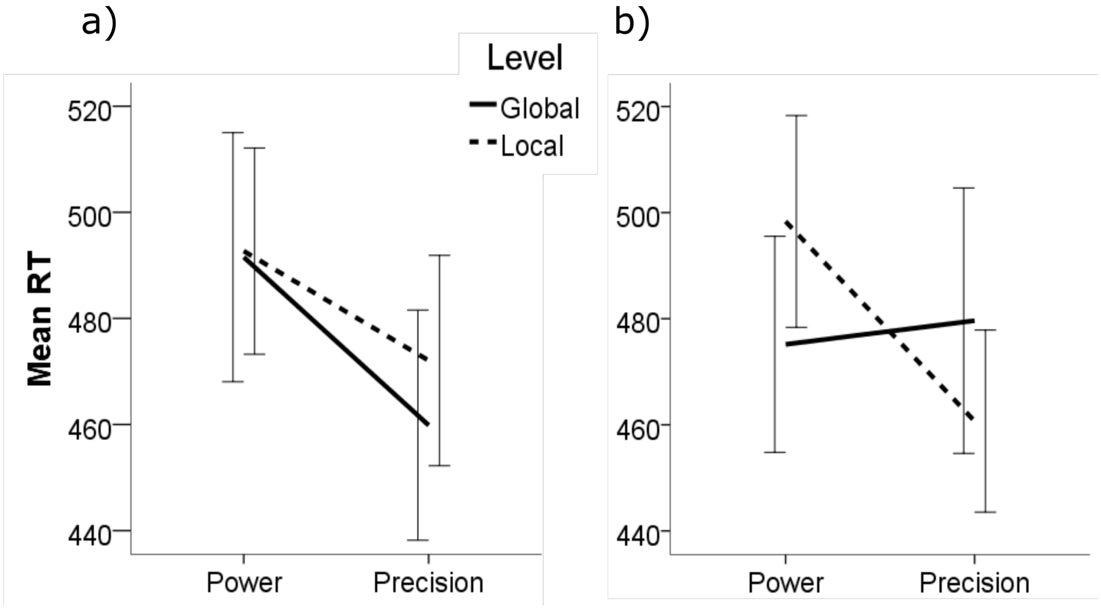

Figure 8. Mean reaction times (ms) for Chapter 3: Experiment 2.
Mean reaction times (RT) in milliseconds to target stimuli presented at the global and local levels of a compound stimulus, separated for power and precision grasping. Responses are made with either the left hand (a) or the right hand (b). Error bars represent +/- 1 SE.

4.4. Discussion

The results from Experiment 2 replicated the core finding of Experiment 1 that local level targets are detected faster following preparation of a precision grasp, relative to a power grasp. This time the effect of grasp preparation was present in the absence of a main effect of target level. The influence that grasp preparation has on the processing of local information is therefore not dependent on the commonly observed global bias in visual processing.

Interestingly, global processing was unaffected by action preparation. Indeed, we expected detection of global targets to be faster following the preparation of power, relative to a precision, grasping actions. Although speculative, this could be due to the non-spatial nature of the motor task (i.e. rather than reaching to grasp a power or precision device, participants held both devices in their hand throughout the task). Local information is thought to be predominantly processed by the ventral visual pathway, while global processing is thought to be processed by the dorsal pathway. Evidence for this segregation comes from studies of patients with lesions to the posterior parietal cortex, a major section of the dorsal pathway. These patients present with a condition called simultanagnosia (Luria, 1959; Rafal, 2003) resulting in a profound inability to processing global visual information, however local processing is largely spared (Kinsbourne & Warrington, 1962). This is in line with the role of the dorsal pathway, in particular the posterior parietal cortex, in processing the spatial relationships between multiple objects and the ventral pathway in object recognition (Ungerleider & Haxby, 1994). Given that the cued actions in these tasks were inherently non-spatial, it is possible that only the ventral visual pathway was modulated by the prepared actions. However, further research is needed to reveal distinct effects of action on ventral and dorsal visual processing.

Unexpectedly, the effect of grasp magnitude on local/global processing in Experiment 2 was only observed in the dominant right hand, compared to Experiment 1 where the effect was not influenced by the hand used to execute the movement. It is unclear why reducing the number of local elements, and in turn the global bias, would limit the effect of grasp preparation on local processing to the right hand. Perhaps the relative increase in the saliency of the local level, predominantly processed by left hemisphere structures (Hübner, 1998; Van Kleeck, 1989), resulted in the right hand specificity of the effect. In addition to this, regardless of the hand used to execute the grasps, precision responses were faster than power responses across both Experiments 1 and 2. This is not in line with the notion that, relative to the right hand, the left hand may be specialized for power grasping (Guiard, 1987).

Previous evidence has shown that action preparation can influence visual perception of stimulus features such as orientation (Bekkering & Neggers, 2002; Hannus et al., 2005) and size (Fagioli et al., 2007; Wykowska & Schubö, 2012). These examples show that visual information is biased toward stimulus features relevant for upcoming action, representing the tight coupling of action and perception. Here, the bias is extended to include hierarchical stimulus features. In contrast to the previous evidence that compared the influence of qualitatively different actions (e.g. grasping vs. pointing) on visual perception of overall feature dimensions relevant to the actions (e.g. orientation/size and colour/luminance), the findings presented here demonstrate a more fine-grained influence whereby varying the magnitude of the same basic grasping action influences subsequent visual processing. This is likely an important aspect of the adaptive control of movement, such that perceptual features most relevant to the upcoming action are facilitated in visual processing, compared to less relevant features.

Given that reaction times to local/global target stimuli in the tasks were gathered from execution of the cued movement itself, it is possible that perception of the local/global target facilitated the action, rather than the inverse. It seems unlikely that the reaction time effects observed here reflect *visual-motor*, rather than *motor-visual*, priming for a number of reasons. First, participants are always cued to prepare the grasp 1000ms before the onset of the compound stimulus, so visual-motor priming would imply a strategy of inhibiting a movement cue that is highly informative, until after onset of the compound stimulus. Nevertheless, it is conceivable that visual-motor priming is contributing to some extent to the reaction time effects of grasping on local/global target detection presented here.

5. Chapter Overview

Recent findings have shown that not only can the perception of objects prime associated actions, but the reverse is also true: preparing actions can prime the perception of associated stimulus features. These findings have shown that planning simple reaching and grasping movements can bias the perception of stimulus orientation (Craighero et al., 1999), size (Symes et al., 2008) and apparent motion (Lindemann & Bekkering, 2009).

In this chapter, two experiments investigated an extension of effects of action planning on perception to a previously unstudied feature of hierarchical stimulus structure. Participants prepared power or precision grasping actions while detecting a target stimulus that could appear at either the global or the local level of a hierarchical stimulus. Targets presented at the local level were detected faster following the preparation of a precision grasp, compared to a power grasp (Exp. 1). However, selection of targets presented at the global level was unaffected by the prepared action. Furthermore, this effect was not influenced by the relative saliency of the global level (Exp. 2). Overall, the findings suggest that preparing to make variations in the same basic action (a grasp) can selectively influence detection of a subsequent visual local target.

Chapter 4: AN ELECTROPHYSIOLOGICAL INVESTIGATION OF ACTION-MODULATED SIZE AND LOCAL/GLOBAL PROCESSING[3]

1. Abstract

Preparing simple actions can facilitate reaction times to stimuli that contain an action-relevant perceptual feature. Previous studies have shown that target stimuli are detected faster if they are presented at the location of an upcoming reaching action, are orientated in the same direction as a grasping action, or if their size matches the aperture of a grasping action. This influence of action on perception is assumed to reflect mechanisms of selection in visual perception tuned to current action goals, such that action relevant sensory information is prioritized relative to less relevant information. The neural mechanisms of effects of action on perception of stimulus features are poorly understood. Here, event-related potentials (ERPs) elicited by task-irrelevant stimuli varying in their relative size (large vs. small) were compared during the preparation of power and precision grasping actions. Early ERP components elicited by the stimuli were enhanced for larger probes during power grasp preparation and smaller probes during precision grasp preparation. Additionally, local targets were also detected faster following precision, relative to power grasp cues. The results demonstrate a direct influence of grasp preparation on sensory processing of size and provide further evidence that the hierarchical dimension of objects may be a relevant perceptual feature for grasp programming.

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[3] The findings from this chapter have been published in *Cortex* (Job, van Velzen, & de Fockert, 2017)

2. Introduction

In Chapter 3, motor-visual priming of local/global stimulus features was investigated in two experiments. In Experiment 1, participants were required to detect a target stimulus presented at the local or global level of a compound stimulus following a cue to prepare either a power or precision grasp. The magnitude of the prepared grasp (power vs. precision) biased visual processing toward stimulus features relevant for the upcoming action, such that detection of local targets was facilitated during the preparation of precision grasping relative to power grasping. In Experiment 2 (Chapter 3), the effect was replicated under conditions in which the saliency of the global level was reduced, suggesting that the effect is not dependent on the commonly observed global bias in visual processing. These findings add to the now numerous behavioural observations of effects of action preparation on vision, however the neural correlates of motor-visual priming remain largely unknown.

One motor-visual priming study to date used electrophysiology (Wykowska & Schubö, 2012) combined with a movement task (grasping vs. pointing) and a visual search for size and luminance targets. That study found facilitated performance on action-perception 'congruent' conditions (i.e. grasping facilitated size targets and pointing facilitated luminance targets). This pattern was reflected by a modulation of early event-related potential (ERP) components, providing supporting evidence that action affects early perceptual processing. That study found that qualitatively different actions (i.e., grasping vs. pointing) can prime different feature dimensions (size vs. luminance), demonstrating a large-scale effect of action preparation on visual processing. However, it remains unclear whether preparing different versions of the same basic action can also lead to subsequent differences in visual processing. If action preparation indeed tunes incoming sensory information toward features relevant to the prepared action, then specific perceptual features (e.g. large vs. small objects) should be modulated, as well as the broader feature dimensions (e.g. size vs. luminance) previously investigated (Wykowska & Schubö, 2012).

The experiment in this chapter utilises the fine temporal resolution of EEG to investigate the effects of grasp preparation on processing of visual size, aiming to directly demonstrate a selective effect of grasp preparation on early stages of visual processing. This experiment also enabled a further investigation of the behavioural effects of global/local processing during grasp preparation using this adapted experimental design.

Similarly to Experiments 1 and 2 (Chapter 3), participants were cued to prepare a power or precision grasp before being presented with a compound stimulus. Also, as in the experiments of Chapter 3, they were instructed to detect a target shape that could appear at either the local or the global level of the compound stimulus, or it could be absent from the display. On two thirds of trials, during the cue-target interval, a task-irrelevant visual probe was presented that could either be relatively small or large. In visual processing, enhanced ERP components have been observed in response to a task-irrelevant visual probe stimulus presented in an attended area relative to an unattended area of space (Hillyard, Vogel, & Luck, 1998; Hillyard & Anllo-Vento, 1998). Similar effects have been observed at the goal location of eye movements (Eimer et al., 2006a, 2007) and at effector and goal locations of reaching movements during movement preparation (Gherri et al., 2009; Job et al., 2016; Mason et al., 2015) reflecting an adaptive modulation of sensory processing tailored to the specific movement being prepared. Recent data suggest that the early P1/N1 components can also reflect a biasing mechanism operating on processing of other stimulus features, not just spatial locations (Karayanidis & Michie, 1997; Valdes-Sosa et al., 1998; Zhang & Luck, 2009). If the behavioural effects of grasp preparation reflect a similar adaptive sensory modulation we would expect that early event-related potentials elicited by the visual probes should be modulated in line with the probes' compatibility with the prepared grasp. This would mean that early components (P1 and N1) elicited by the large probe should be enhanced in amplitude during the preparation of a power grasp relative to a precision grasp, while the components elicited by the small probe should be enhanced during precision relative to power grasps.

3. Experiment 1

3.1. Participants

A total of 16 adults (13 female) with a mean age of 25 years (SD = 3.85) participated in return for £10. All participants were right handed (mean laterality quotient = 87.06, SD = 17.00) and reported normal or corrected to normal vision. The Local Ethics Committee at Goldsmiths, University of London, approved all experimental protocols and the experiment adhered to the ethical guidelines presented in the 1964 declaration of Helsinki. All participants provided written informed consent before the beginning of each experiment and were debriefed at the end of the experiment as appropriate.

3.2. Stimuli & task

Figure 9 shows the trial procedure. The stimuli and task were identical to Experiment 2 (Chapter 3), except for the following aspects: At 1000ms following the cue prompting participants to prepare either a precision or a power response, a task-irrelevant visual probe stimulus was presented that could be either relatively large (4.8° visual angle), relatively small (1.6° visual angle) or absent with equal probability. Probes were presented for a duration of 100ms. At 600ms after probe onset, the compound stimulus was presented for 250ms. Following an error (incorrect grasp) or a time-out (no response within 1200ms) a feedback tone was delivered via two speakers symmetrically aligned in front of participants.

The contrast of the presentation was also reversed, compared to Experiment 2 (Chapter 3) with white stimuli presented on a black background. Stimuli were presented using the Psychophysics Toolbox extensions (Brainard, 1997) version 3.0.12 implemented in MATLAB (R2014b, version: 8.4).

3.3. Procedure

Following provision of written consent and the (revised) Edinburgh Handedness Inventory (Veale, 2014), participants completed a practice block of 30 randomised trials, followed by eight blocks of 100 randomised trials with self-timed breaks between blocks. Targets (local/global) were presented with equal probability on 80% of trials (640) and were absent from the display on 20% of trials (160). Size probes (large/small) were presented with equal probability on 60% of trials (480). Probe-present trials were grouped into four conditions (100 trials each) according to the size of the probe (large/small) and the grasp cue (power/precision), regardless of the target level (global/local/absent). These conditions were used for the ERP analysis of the probe evoked activity. For a behavioural analysis similar to that of Chapter 3 (Exp. 1 and 2), trials in which a target was present in the hierarchical stimulus, but size probes were absent (40% of total trials) were grouped into four conditions (80 trials each) determined by the factors of grasp cue (power/precision) and target level (global/local). Trials in which both a target and a size probe were presented made up 40% of total trials (320) and were divided into eight conditions (40 trials each) determined by the factors of grasp cue (power or precision), probe size (large/small) and the target level (global/local). The experimental task lasted approximately 45 minutes. The mapping between the colour of the cue (blue/green) and the grasp (power/precision) was counterbalanced across participants. Given that effects of interest were limited to the right hand in Experiment 2 (Chapter 3), only right-hand responses were recorded in this experiment.

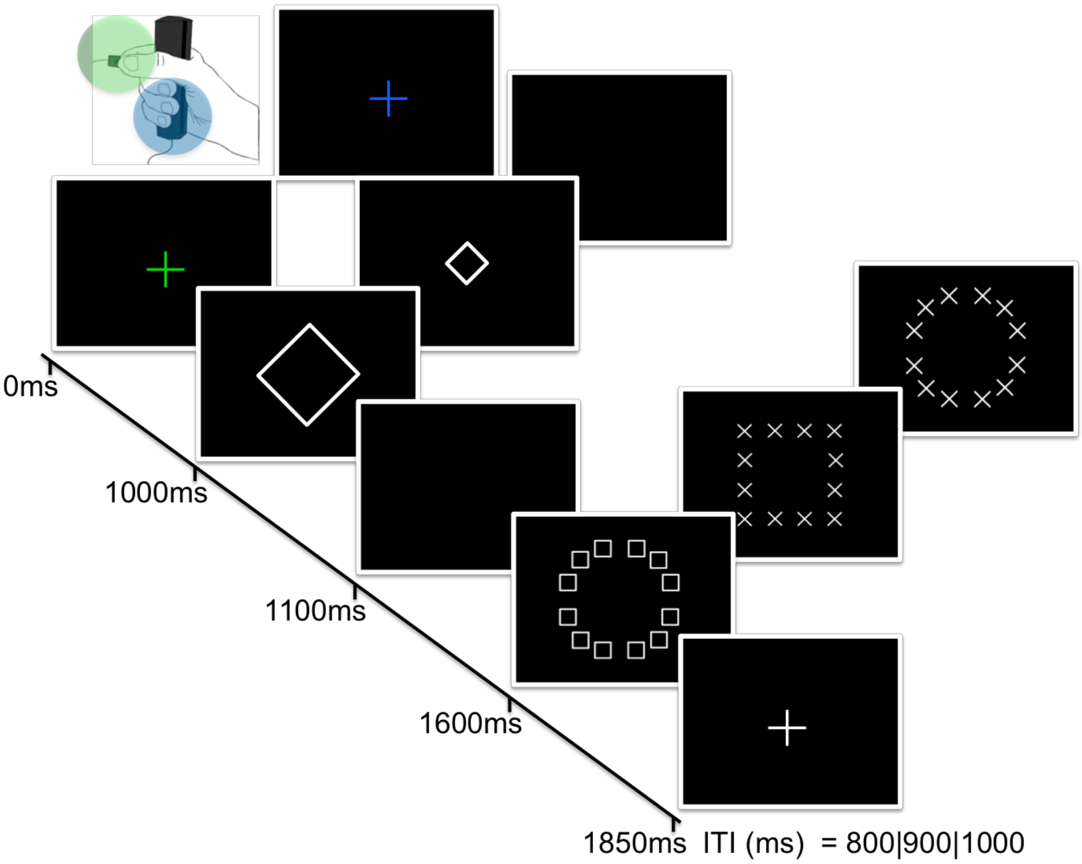

Figure 9. Trial procedure for Chapter 4: Experiment 1.
Schematic illustration of the trial procedure with alternate possibilities superimposed above. Following the coloured precision or power grasp cue at the start of each trial, a large, small or absent probe was presented for 100ms. At 600ms after probe onset, a compound stimulus was presented for 250ms that could contain a target shape (e.g. square) at the local or global level, in which case participants executed the cued grasp. If the target was absent, the prepared grasp had to be withheld. The inter-trial interval (ITI) was randomly varied to be 800ms, 900ms or 1000ms. Images are not to scale.

3.4. EEG recording, processing & analysis

Chapter 2 outlines in detail the equipment and pre-processing pipeline used to record and analyse the EEG data, therefore only a brief summary of the analysis is provided here.

Continuous EEG data were divided into 700ms epochs locked to the onset of the probe including a 100ms pre-stimulus baseline. Epochs including voltages exceeding + and/or -100μV were automatically rejected prior to analysis. Eye-blink artefacts were corrected for using Independent Component Analysis (ICA). The mean amplitudes of ERP components within pre-defined time windows were extracted for analysis. The mean positive amplitude between 70 and 110ms post probe onset was extracted as the P1 mean amplitude. The mean of negative amplitudes between 130-170ms post probe onset was extracted as the N1 mean amplitude. Peak measures were extracted from electrode sites PO7 and PO8, which elicited the largest ERPs as observed in scalp maps of averages over all conditions. The difference between the mean P1 and N1 values was computed to obtain a mean peak-to-peak amplitude measure of the N1 component.

For the statistical analysis, the mean peak-to-peak amplitudes of the N1 component evoked by probe stimuli were analysed in a 2x2x2 repeated measures ANOVA with factors of grasp magnitude (power/precision), probe size (large/small) and electrode hemisphere (PO7/PO8).

3.5. Results

For the behavioural analysis, correct reaction times to targets presented at the global and local dimension of the compound stimuli were compared using a 2x2x2 repeated measures ANOVA with factors of target level (local/global), grasp (power/precision) and probe (large/small).

Figure 10 shows the mean reaction times for local and global targets presented after a large (a) or small (b) probe stimulus as well as after no probe was presented (c). A main effect of grasp magnitude was found with faster precision (M = 440, SD = 74.15) compared to power (M = 473, SD = 68.68) grasp responses by 33ms (SE = 5.46), $F(1, 15) = 35.55$, $p < .001$, $\eta_P^2 = .703$. A main effect of target level was also found with faster responses for global (M = 448, SD = 77.77), compared to local targets (M = 465, SD = 78.26) by 17ms (SE = 5.63), $F(1, 15) = 8.85$, $p = .009$, $\eta_P^2 = .371$. A significant interaction between target level and size of the probe was observed, $F(1, 15) = 14.56$, $p = .002$, $\eta_P^2 = .493$. The interaction between grasp magnitude and target level did not reach statistical significance ($F(1, 15) = 2.09$, $p = .169$, $\eta_P^2 = .122$) and neither did the interaction between grasp magnitude and probe size $F(1, 15) = .805$, $p = .384$, $\eta_P^2 = .051$. However a significant interaction between target level, grasp magnitude and probe size was found, $F(1, 15) = 13.80$, $p = .002$, $\eta_P^2 = .479$. This indicates that the mean reaction times to global/local target stimuli were influenced both by the relative size of the task-irrelevant probe preceding the target as well as the prepared grasp. To investigate this interaction further, three 2x2 ANOVAs with factors of grasp magnitude (power/precision) and target level (global/local) were used for each probe condition (large/small/absent) separately.

Following the presentation of a large probe stimulus (Figure 10 panel a) the interaction between grasp magnitude and target level was significant ($F(1, 15) = 7.46$, $p = .015$, $\eta_P^2 = .332$) and post-hoc t-tests confirmed that responses to local targets were faster using a precision grasp (M = 443, SD = 61.51), compared to a power grasp (M = 489, SD = 63.92) by 46ms (SEM = 6.15), $t(15) = 7.50$, $p < .001$. This difference was not significant for global targets, $t(15) = 1.01$, $p = .331$. The interaction between grasp magnitude and target level was not significant following small probes (Figure 10 panel b) , *F*(1, 15) = .251, p = .624, η_P^2 = .016. Similarly, an ANOVA with factors of grasp magnitude (power/precision) and target level (global/local) was used for probe absent trials (Figure 10 panel c) and revealed no significant interaction between grasp magnitude and target level, *F*(1, 15) = 2.50, p = .135, η_P^2 = .143.

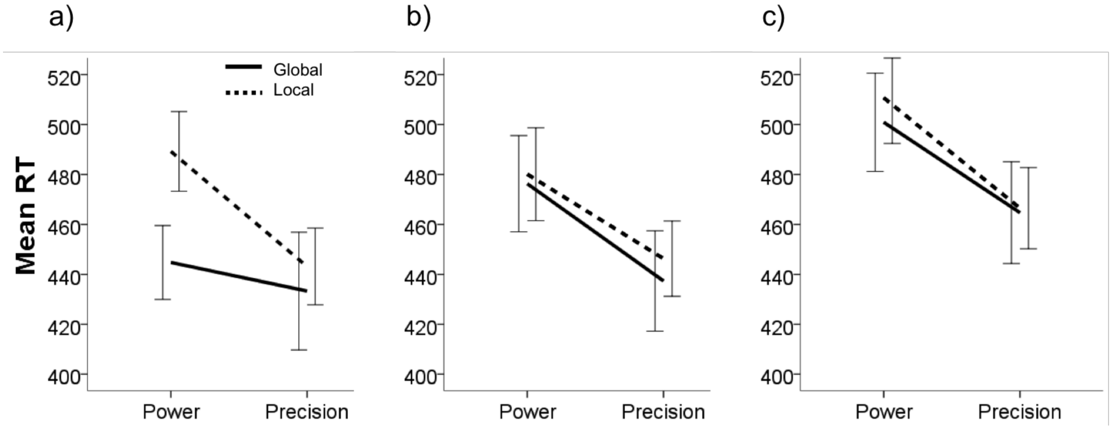

Figure 10. Reaction time results for Chapter 4: Experiment 1.
Mean reaction times (RTs) in milliseconds to targets presented at the global (solid line) and local (dotted line) level of compound stimuli, separated for power and precision grasp cues. Compound stimuli are presented following a large (a), small (b), or no probe stimulus (c). Error bars represent +/- 1 SE.

Errors were made on an average of only 3.3% of trials so were not further analysed (see Table 2 for a details of error rates across each condition).

Table 2. Error rates (%) with standard deviations for Experiment 1 Chapter 4

	Global Target	Local Target
Power	3.20 (2.14)	3.13 (3.35)
Precision	3.67 (2.56)	3.05 (2.33)

Figure 11 shows the grand averaged event-related potentials (ERPs) elicited by the task-irrelevant probe stimuli. For the N1 mean peak-to-peak amplitude, no main effects of grasp magnitude (power/precision), probe (large/small) or electrode hemisphere (PO7/PO8) were observed (*F*(1, 15) = .92, p = .352, η_P^2 = .058, *F*(1, 15) = 3.28, p = .090, η_P^2 = .108 and *F*(1, 15) = 1.66, p = .217, η_P^2 = .100, respectively). A significant interaction between the size of the probe and the grasp being prepared was observed, *F*(1, 15) = 8.95, p = .009, η_P^2 = .374, as well as a significant interaction between the probe size, grasp magnitude and electrode hemisphere (*F*(1, 15) = 5.10, p = .039, η_P^2 = .254).

Separate two-way ANOVAs with factors of probe size and grasp magnitude were then run for left and right hemispheres, revealing a significant interaction at left hemisphere sites, *F*(1, 15) = 13.54, p = .002, η_P^2 = .474. Post-hoc t-tests confirmed that the mean peak-to-peak size of the N1 component at left electrode sites evoked by large probes was enhanced during the preparation of power grasps (M = 4.22, SD = 4.17), relative to precision grasps (M = 3.15, SD = 4.08), by 1.07μV (SD = 1.00), t(15) = 4.25, p = .001. The reverse effect was observed for the N1 at left electrode sites evoked by small probes, with marginally larger mean amplitudes during the preparation of precision grasps (M = 3.13, SD = 3.17), relative to power grasps (M = 2.37, SD = 3.76) by .76μV (SD = 1.33), t(15) = -2.30, p = .036 (p = .072 following correction for multiple comparisons). At right hemisphere electrode sites the interaction between probe size and grasp magnitude was non-significant, *F*(1, 15) = 2.50, p = .135, η_P^2 = .143.

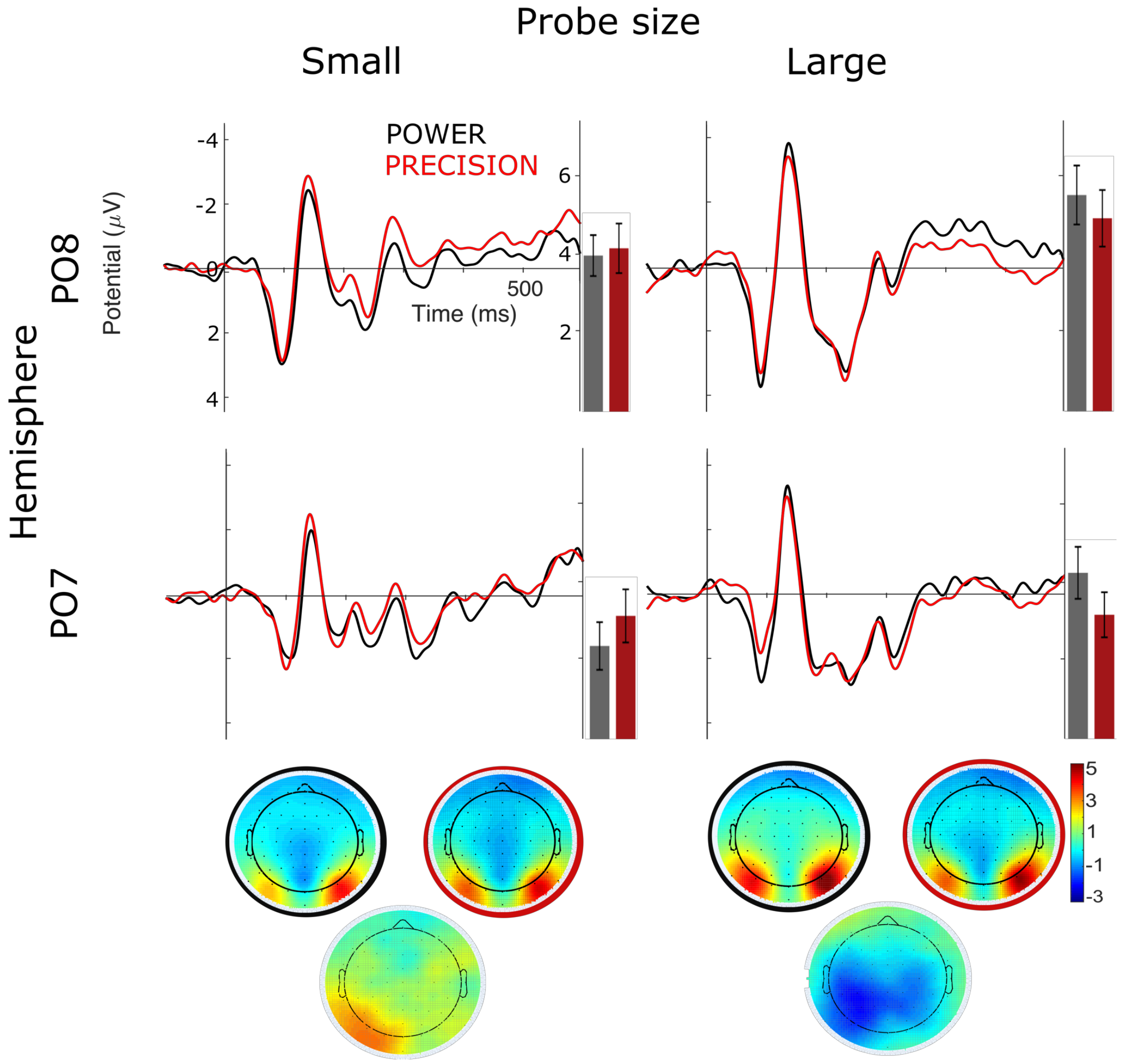

Figure 11. ERP results for Chapter 4: Experiment 1.
Grand-averaged event-related potentials (ERPs) elicited by the probe stimuli (onset = 0ms) during power and precision grasp preparation. Bar graphs show the mean peak-to-peak amplitude of the N1 component during power (grey) and precision (red) grasp preparation (error bars represent +/- 1 SE). Scalp maps show the distribution of the N1 component peak-to-peak amplitude (μV) for each condition (from left to right – small probe power grasp, small probe precision grasp, large probe power grasp, large probe precision grasp) as well as the difference below (power – precision).

3.6. Discussion

The findings demonstrate that grasp preparation can bias early visual ERPs elicited by task-irrelevant probes of varying sizes. The visual N1 component was enhanced for large probes during power, relative to precision, grasp preparation and marginally enhanced for small probes during precision, relative to power, grasp preparation. This demonstrates a direct effect of grasp preparation on early stages of visual processing. Effects of manual reaching and eye movement preparation on sensory processing have been linked to overlapping brain networks involved in action and attention (Astafiev et al., 2003; Maurizio Corbetta, 1998; Maurizio Corbetta et al., 1998b; Maurizio Corbetta & Shulman, 2002). Whether similar links exist for grasping movements remains to be determined and future studies should elucidate the brain mechanism activated by a grasp instruction. Furthermore, a behavioural effect of probe size on local/global target detection was modulated by grasp, such that large (vs. small) probes only facilitated global (vs. local) processing during power (vs. precision) grasp preparation.

Previous ERP evidence for action-modulated vision manipulated the prepared action in blocks, rather than randomly cueing actions on each trial, with one exception (Wykowska & Schubö, 2012), who instead presented the size or luminance targets in separate blocks while varying the cued action trial-by-trial. Our design demonstrated modulated visual information during action preparation where both the cued action (power/precision grasp) and the stimulus feature (large/small or local/global) are manipulated randomly on each trial. This demonstrates a more dynamic adjustment to visual processing as a consequence of action preparation, without the possible confound associated with participant's prior knowledge of the action and/or stimulus feature before trial onset.

Although grasp preparation altered reaction times to the compound stimuli in the experiments of Chapter 3 (Experiments 1 and 2), this was not replicated in the probe-absent trials of this experiment as expected. An effect of approximately 35ms in the experiments of Chapter 3 was reduced to just 10ms in this experiment. Only following a large probe stimulus, was an effect of grasping observed on reaction times to global/local target stimuli in this experiment. A number of differences between the experiments, implemented to better facilitate the use of EEG, may have contributed this loss of effect. For example, additional trial numbers were required, and the contrast was also reversed so stimuli were white on a black background. It is unclear why these factors would influence the effect. One further alteration, the longer cue-target interval (+ 600ms), may have played a role. This additional time which was added to ensure that no-probe trials had the same length as those in which a probe was presented. Modulations of sensory processing in the context of the specific action being prepared have been demonstrated to be temporally dynamic (Mason et al., 2015). Indeed, further research is required to determine how grasp preparation affects sensory processing over time. Finally, the mere presence of the visual probes in this experiment may have affected the action-perception effect in general, even on the probe absent trials. Exactly how action-perception interactions are affected by the context in which they are measured is an intriguing question that warrants further work.

As noted in the Discussion of Chapter 3, it is possible that perception of the local/global target facilitated the action, rather than the reverse. This alternative conclusion seems quite unlikely in the current studies given that the pattern of probe-evoked potential effects show a selective influence of the movement cue on visual processing before onset of the compound stimuli. Nevertheless, it is still conceivable that visual-motor priming is contributing to some extent to the reaction time effects of grasping on local/global target detection presented in this thesis. Separating the cued motor response from the perceptual decision in a dual task design may help to elucidate this further. A detailed discussion of the advantages and disadvantages of single and dual task designs is provided in Chapter 2 (Experimental methods).

Chapter 5: MOTOR PREPARATION AND THE PRIMING OF ORIENTATION PERCEPTION

1. Abstract

There is growing evidence that the preparation of simple actions can influence performance in tasks of visual perception. Previous research has shown that preparing actions speeds responses to action-relevant stimulus features. However, whether reaction time effects reflect an influence on early visual processing or not is not fully understood. Influences on early visual processing are likely to be reflected in changes in perceptual sensitivity to discriminate an action-relevant feature, however due to the use of simple target detection tasks with very high accuracy, effects of action on perceptual discrimination have been precluded. In three experiments, the influence of action preparation on visual discrimination of orientation was investigated. Participants were cued to prepare oriented reach-to-grasp actions before discriminating two spatial frequency gratings as the same or different in orientation. The degree of difference in grating orientation was continuously adapted to participants' performance across the task in order to ensure adequate error rates. As expected, stimuli oriented in the same direction as the prepared grasp (congruent) were responded to faster than incongruently oriented stimuli. However, action preparation had no influence on perceptual sensitivity. This was true across two levels of discrimination difficulty, as well as across two cue-target intervals. This suggests that action preparation may not influence early visual processing but may instead influence higher order response or decision related processing.

2. Introduction

It is well known that actions can be automatically primed by the visual properties of objects such as their spatial location, orientation and size (Craighero, Fadiga, Umilta, & Rizzolatti, 1996; Hommel & Prinz, 1997; Tucker & Ellis, 1998; Vogt & Thomaschke, 2007). However the reverse effect is also possible, such that motor processing itself also influences the processing of incoming perceptual information, effects often termed *motor-visual priming* (Craighero, Fadiga, Rizzolatti, & Umilta, 1999). So far, the evidence for motor-visual priming has shown that preparing simple actions such as reaching and grasping can influence visual perception of features relevant to the action, (e.g. location, size, orientation or motion). For example, stimuli are responded to faster if they are oriented in the same direction as a prepared grasping action (Craighero et al., 1999), or the stimuli's relative size is consistent with the prepared grasping action (Symes et al., 2008). Similarly, if stimuli appear to rotate in the same direction as a manual object rotation (Lindemann & Bekkering, 2009) they are detected faster. These findings suggest that prepared actions can alter the perception of action-relevant stimulus features, thus demonstrating a the tight, and bidirectional, coupling between action and perception.

Reaction time effects, however, can be attributed both to changes in perceptual processing, or to shifts in decision/response related processing. The focus on reaction time effects is largely due to the use of rather easy detection tasks that result in very low error rates. Whether the effects of motor-visual priming reflect changes in sensory perception, or instead shifts in decision/response related processing is therefore unclear (Reed, 1973; Santee & Egeth, 1982; Wickelgren, 1977). If the effect of action on perception operates early in sensory perception, then sensitivity to discriminate the action relevant feature should be influenced.

In this chapter, three experiments investigated whether action preparation influences perceptual sensitivity as well as speeded responses. To do this, participants were required to discriminate two briefly and simultaneously presented spatial frequency gratings as the same or different in orientation. Unlike previous studies the difference between the gratings was continually updated throughout the task depending on each participant's performance. This ensures adequate error rates to measure perceptual sensitivity, as well as reaction times. Importantly, before stimuli onset, participants were cued to prepare one of two grasping actions, oriented either towards the right or the left. The orientation of the prepared grasp (rightward or leftward) and the orientation of the gratings (both rightward or both leftward) could be either congruent or incongruent on any given trial. If action relevant features are prioritized not only in terms of processing speed, but also in terms of perceptual sensitivity, then discrimination of the gratings should improve following a cue to prepare a congruently oriented grasping action, relative to an incongruently oriented grasping action.

Furthermore, orientation discrimination was measured across two levels of perceptual difficulty by varying the degree of difference between the gratings to be relatively large (easy to discriminate) or relatively small (difficult to discriminate). If effects of action on perception depend on the perceptual resources currently available, then motor-visual priming effects should vary as a function of difficulty. There are only very few and rather inconsistent findings in the literature regarding perceptual difficulty in motor-visual priming. For example, some have shown that effects of action on perception in a task of visual search can vanish with larger set sizes (Bekkering & Neggers, 2002; Hannus et al., 2005), suggesting that action is only capable of influencing perception when sufficient perceptual resources are available. However, more recently similar effects of action preparation on orientation change detection across three levels of difficulty (Gutteling et al., 2011) have been reported, suggesting no influence of perceptual difficulty. To help clarify these inconsistent findings a manipulation of perceptual difficulty was included in the experiments of this chapter.

As mentioned in the General Introduction, in a related set of paradigms, perceptual sensitivity (*d'*) in the context of action preparation has been investigated. In these tasks different types of manual actions are typically prepared (e.g. grasping, reaching or pointing) before participants discriminate feature *dimensions* such as size, orientation or color. These studies have demonstrated that action planning can not only speed responses but can also sharpen estimations of stimulus size (Bosco et al., 2017) as well as orientation (Gutteling, Kenemans and Neggers, 2011). However, these studies have focused on priming feature perception at a more general *dimension* level. Whether specific features (i.e. leftward rightward orientation) can become flexibly prioritized in the context of action preparation is of primary concern here.

3. Experiment 1

3.1. Participants

22 adults (17 females, mean ± SD of age: 27 ± 4.38 years) participated in the experiment. This sample size is capable of detecting even moderate effect sizes (η_P^2 =0.32) as previously reported using a very similar paradigm (Gutteling, Kenemans & Neggers, 2011) with .85 statistical power to reject the null hypothesis, given a critical threshold of .05 (two-tailed). All participants were right handed (mean laterality quotient (Veale, 2014) = 92.05, SD = 14.19) and reported normal or corrected to normal vision. The Local Ethics Committee at

Goldsmiths, University of London, approved all experimental protocols and the experiment adhered to the ethical guidelines presented in the 1964 declaration of Helsinki. All participants provided written informed consent before the beginning of each experiment and were debriefed at the end of the experiment as appropriate. Participants received either course credits or £10 for taking part in the study.

3.2. Stimuli & task

Spatial frequency gratings (4 cycles/degrees, contrast 100%, 4.5° eccentricity) were displayed on the horizontal meridian, on the left and right side (37% and 63% of the screen width, respectively) of a central white fixation dot (visual angle 6°) on a grey background (see Figure 12). Stimuli were generated using MATLAB 2012a (64 bit) and presented using the Psychophysics Toolbox Version 3.0.8 (Brainard, 1997).

Figure 12 shows a schematic illustration of the trial procedure. Each trial was initiated by holding the lever device with the right hand. A movement cue ("R" or "L") was then presented on the screen, indicating which grasp should be prepared. Following the movement cue, two gratings were presented for 250ms, which could be orientated either congruently, or incongruently with the orientation of the prepared grasp (see Figure 12 panel b). Both the orientation of the gratings (left/right) and the movement cue were varied randomly on each trial. Participants were instructed to lift the hand from the lever device and execute the prepared leftward or rightward grasp only if the orientation of the two gratings was the same (i.e. 0° difference). Auditory feedback (200 Hz tone for a duration of 100ms) was presented following an error.

Responses were collected from a custom-built device (HxWxD: 30cm x 30cm x 32cm) with two graspable cubes (5cm x 5cm x 5cm) mounted to it on the upper left and right corners (see Figure 1c). The cubes were tilted 45° and 315° such that to grasp them required participants to orient their grasp either leftwards or rightwards. A depressible button was integrated into each cube in order to record information about grasping responses. A lever device (4cm x 9cm x 11cm) was also placed in front of participants equidistant from the left and right grasping cubes. Pressing and holding the lever initiated each trial. The time elapsed between target onset and the time at which the lever was released (reaction time) as well as the time at which the grasp was made (movement time) was recorded. Accuracy of reporting the stimulus orientations as the same or different as well as the accuracy of the grasp was also recorded.

Throughout the task, the orientation discrimination level was determined adaptively using Palamedes toolbox (http://www.palamedestoolbox.org). A "four-correct-then-down/one-wrong-then-up" staircase procedure was used (Luntinen, Rovamo, & Näsänen, 1995). This ensured that perceptual discrimination was above chance, while allowing for adequate error rates for analysis. In line with previous research (Bartolucci & Smith, 2011), six staircase steps were established with each step consisting of two orientation differences ('small' and 'large'), that were always separated by 5°. Reference stimuli were either 5° or 60° from vertical 0° clockwise or counter clockwise. Therefore, the difference from the reference stimuli, either clockwise or counter clockwise, on any given trial could be; 22°/27° (staircase step 1), 19°/24° (step 2), 16°/21° (step 3), 13°/18° (step 4), 10°/15° (step 5), 7°/12° (step 6). Within each staircase step one of two differences in degree could be presented (e.g. in staircase step 1 either 22° or 27° clockwise or counter clockwise) in order to manipulate the difficulty of the perceptual discrimination as either relatively large (e.g. 27° difference) or relatively small (e.g. 22° difference).

3.3. Procedure

Participants sat in a dimly lit room, 57 cm from the monitor, which was placed above the response device. Participants first completed a practice block of 20 trials, followed by six blocks of 86 trials with self-timed breaks between blocks. Trials were randomly selected from within the given staircase step. Trials could contain a rightward (50% of trials) or leftward grasp cue (50% of trials), followed by a congruent (50% of trials) or incongruently (50% of trials) oriented pair of gratings. Gratings could be identical to each other in their orientation (50% of trials), different by a small degree (25% of trials) or different by a large degree (25%). Responses were therefore required on 50% of trials where the gratings were identical in their orientation. The entire session lasted approximately 50 minutes.

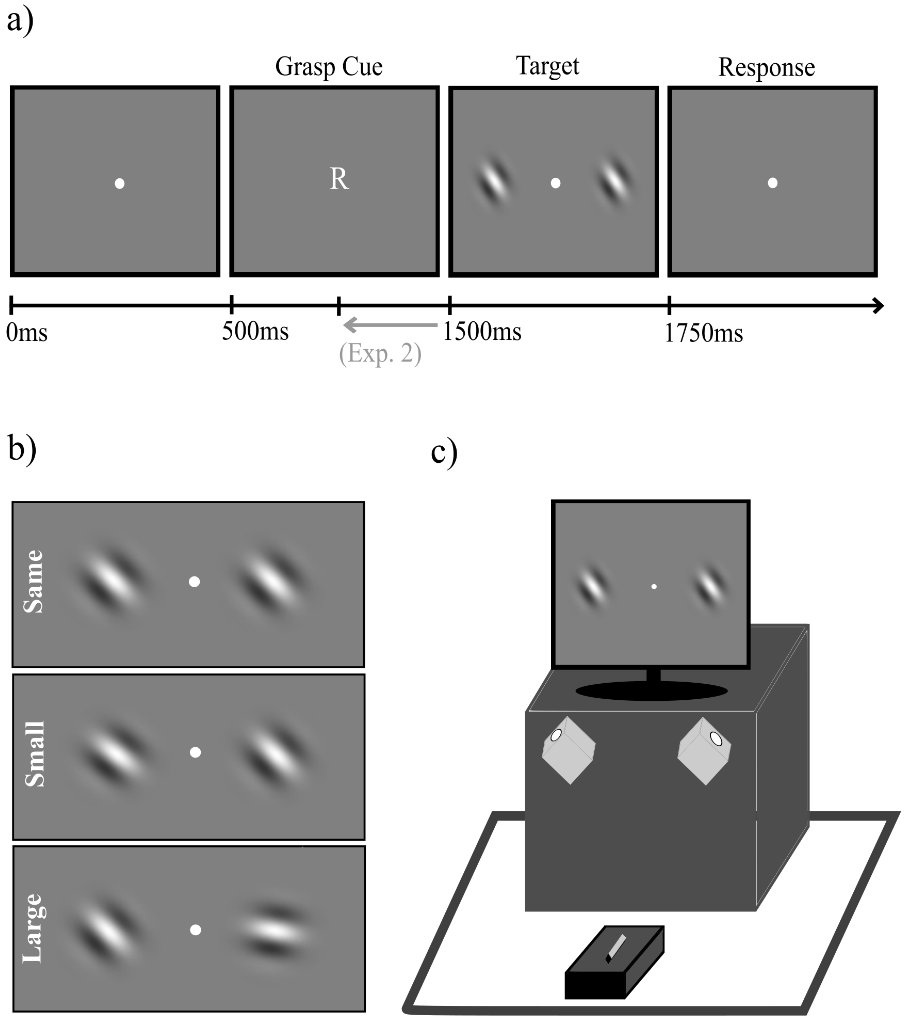

Figure 12. Trial procedure, stimuli and apparatus for Chapter 5: Experiment 1-3.
a) Illustration of the trial procedure. Participants are instructed to fixate on the central dot throughout the task. A rightward ('R') or leftward ('L') cue informs participants which grasp to prepare before spatial frequency gratings are presented. Participants execute the cued grasp if they perceive the gratings to be identical in orientation. In Experiment 3 participants execute the cued grasp only if they perceive the gratings to be different in orientation. b) Examples of leftward oriented spatial frequency gratings either side of a fixation dot that are the same in orientation (upper panel), different by a small degree of orientation (middle panel) and different by a large degree of orientation (lower panel). c) Illustration of the response device used. Two graspable cubes with response buttons mounted to the top left/right corners and angled at 45° and 315° to afford leftward/rightward oriented grasps. The lever device initiated each trial when pressed.

3.4. *Data analysis*

For reaction time data, only trials in which a correct grasping response was made and the reaction time fell within ± 2.5 standard deviations of the mean were included in the analysis. This resulted in a mean of 2.1% (SD=.79) trials rejected. A within-subjects Analysis of Variance (ANOVA) with a factor of grasp congruency (congruent/incongruent) was then used.

For accuracy data, a within-subjects ANOVA with factors of grasp congruency (congruent/incongruent) and orientation difference (small/large) was used for perceptual sensitivity values. Sensitivity (d') was calculated by subtracting z-transformed false alarm rates (proportion of trials in which gratings that differ were responded to) from hit rates (proportion of trials in which gratings with 0° difference were responded to). Therefore d' = Z(H) - Z(FA), where 'H' is the hit rate, 'FA' is the false alarm rate and 'Z()' denotes the z-transformation. Z-transformed false alarm rates for small and large orientation differences were subtracted from the hit rates separately to calculate sensitivity values for these conditions.

3.5. *Results*

Grasp congruency significantly modulated reaction times with faster responses to gratings with grasp congruent orientations (M = 1237ms, SE = 34.67) compared to incongruent (M = 1267ms, SE = 36.99), $F(1, 21) = 17.00$, $p < .001$, $\eta_p^2 = .447$.

Orientation difference significantly modulated sensitivity ($F(1, 21) = 208.88$, $p < .001$, $\eta_p^2 = .909$) with lower sensitivity for stimuli with the smallest difference in orientation (M = 1.99, SE = .05) compared to those with large differences (M = 2.67, SE = .07). Grasp congruency did not modulate accuracy ($F(1, 21) = .01$, $p = .913$, $\eta_p^2 = .001$), and did not interact with orientation difference ($F(1, 21) = 2.95$, $p = .100$, $\eta_p^2 = .123$). Table 3 shows the means and standard deviations across conditions. As the task was to respond when the stimuli were the same in orientation as each other, hit rates and reaction times for orientation different conditions as well as false alarms and d' for the 0° difference condition are not possible.

Table 3. Accuracy and reaction times for Experiment 1 Chapter 5

	Difference	**Congruent**	**Incongruent**
Hits	**0°**	.90 (.06)	.91 (.05)
False alarms	**Small**	.29 (.06)	.27 (.07)
	Large	.10 (.05)	.11 (.07)
Sensitivity (d')	**Small**	1.94 (.35)	2.03 (.29)
	Large	2.70 (.45)	2.63 (.36)
Reaction times	**0°**	1237 (163)	1268 (173)

3.6. Discussion

In Experiment 1, participants responded when they perceived two spatial frequency gratings as identical in orientation (0° difference) with a pre-cued grasping action. Responses were faster when the gratings were oriented in the same direction as a prepared grasping action (congruent), compared to the opposite direction (incongruent). This is in line with previous findings that grasping actions are initiated faster when signaled by a congruently oriented stimulus (Craighero et al., 1999; Lindemann & Bekkering, 2009).

However, no differences in accuracy or perceptual sensitivity were observed for grasp congruent and incongruent perceptual discriminations.

In Experiment 1, the onset of the perceptual stimulus was fixed at 1000ms after the initiation of action preparation, yet the temporal overlap between actions and perceptual stimuli may be critical in determining the magnitude of effects of action on perception (Zwickel et al., 2007). The perceived direction of motion could be biased by a concurrently produced action, however the bias decreased at longer delay intervals between the onset of the movement and the imperative stimulus (Zwickel et al., 2007), suggesting that effects of action on perception could be proportional to the amount of temporal overlap between the produced and perceived events.

Therefore in Experiment 2, the onset of the perceptual stimulus relative to the movement cue was reduced from 1000ms to 500ms. If effects of priming are maximal when there is a greater overlap between action preparation and stimulus processing, then perceptual discrimination may be affected at a shorter cue-stimulus interval.

4. Experiment 2

4.1. Participants

22 adults (16 females, mean ± SD of age: 23 ± 5.00 years) took part in this experiment. All participants were right handed (mean laterality quotient (Veale, 2014) = 89.20, SD = 14.58) and reported normal or corrected to normal vision. The Local Ethics Committee at Goldsmiths, University of London, approved all experimental protocols and the experiment adhered to the ethical guidelines presented in the 1964 declaration of Helsinki. All participants provided written informed consent before the beginning of each experiment, and were debriefed at the end of the experiment as appropriate.

4.2. Stimuli & task

The stimuli and task were identical to those of Experiment 1, except that the onset of the spatial frequency gratings was 500ms after the movement cue, rather than 1000ms as in Experiment 1 (Figure 12 panel a).

4.3. Procedure

The procedure was identical to that of Experiment 1.

4.4. Data Analysis

The analysis was identical to that of Experiment 1 and a mean of 2.2% (SD=.786) of trials were rejected for either having reaction times that fell outside ± 2.5 SD of the mean or where a grasping error was made.

4.5. Results

Grasp congruency significantly modulated reaction times with faster responses to gratings with grasp congruent orientations (*M* = 1277ms, *SE* = 38.49) compared to incongruent (*M* = 1298ms, *SE* = 38.22), *F*(1, 21) = 7.29, *p* = .013, η_P^2 = .258.

Orientation difference significantly modulated accuracy (*F*(1, 21) = 179.37, *p* < .001, η_P^2 = .895) with lower sensitivity for stimuli with the smallest orientation difference (M = 1.98, SE = .05) compared to those in the large difference condition (*M* = 2.85, *SE* = .09). Grasp congruency did not modulate accuracy (*F*(1, 21) = .01, *p* = .909, η_P^2 = .001), and did not interact with orientation difference (*F*(1, 21) = .45, *p* = .512, η_P^2 = .021).

Table 4. Accuracy and reaction times for Experiment 2 Chapter 5

	Difference	Congruent	Incongruent
Hits	**0°**	.91 (.05)	.90 (.05)
False alarms	**Small**	.29 (.08)	.27 (.06)
	Large	.08 (.05)	.09 (.06)
Sensitivity (d')	**Small**	1.97 (.37)	2.00 (.30)
	Large	2.88 (.51)	2.82 (.58)
Reaction times	**0°**	1277 (181)	1298 (179)

4.6. Discussion

In Experiment 2 the delay between the movement cue and the to-be-discriminated stimuli was half that of Experiment 1, however the same effects were observed. That is, responses were faster when the gratings were oriented in the same direction as a prepared grasping action (congruent), compared to the opposite direction (incongruent). This suggests that a greater overlap between perceived and produced events did little to influence effects of action on perception. However, only two time points following the movement cue were investigated in Experiment 1 (1000ms) and Experiment 2 (500ms), representing only a very course temporal profile.

Importantly, no effect of action preparation was observed on the sensitivity to discriminate the stimuli, as in Experiment 1. In order to investigate the reaction time congruency effect observed in both Experiments 1 and 2 in further detail Experiment 3 instructed participants to respond only when the gratings were different in orientation, rather than identical. This simple change to the task instructions permitted the analysis of reaction times as a function of discrimination difficulty, as well as grasp congruency.

5. Experiment 3

5.1. *Participants*

22 adults (16 females, mean ± SD of age: 24 years ± 3.97 years) took part in the experiment. All participants were right handed (mean laterality quotient (Veale, 2014) = 92.02, SD = 14.24) and reported normal or corrected to normal vision. The Local Ethics Committee at Goldsmiths, University of London, approved all experimental protocols and the experiment adhered to the ethical guidelines presented in the 1964 declaration of Helsinki. All participants provided written informed consent before the beginning of each experiment and were debriefed at the end of the experiment as appropriate.

5.2. *Stimuli & task*

The stimuli and task were identical to those of Experiment 1, except that participants were instructed to respond only when the grating stimuli were different in orientation, and to make no response when they were identical.

5.3. *Procedure*

The procedure was identical to Experiment 1.

5.4. *Data analysis*

The analysis was identical to that of Experiment 1 and 2 and a mean of 3.6% (SD=.90) of trials were rejected for either having reaction times that fell outside ± 2.5 SD of the mean or where a grasping error was made.

5.5. Results

Table 5 shows the mean accuracy, sensitivity and reaction times for each condition. A main effect of grasp congruency was present with faster reaction times for grating stimuli that were congruent with the cued grasp (M = 1166ms, SE = 28.23), compared to incongruent (1184ms, SE = 30.65), *F*(1, 21) = 10.23, p = .004, η_P^2 = .328. A main effect of orientation difference was also observed with faster reaction times to gratings with large differences (M = 1160ms, SE = 29.14) compared to small (M = 1190ms, SE = 29.74), *F*(1, 21) = 34.59, p < .001, η_P^2 = .622. No interaction between grasp congruency and orientation difference was found, *F*(1, 21) = 2.42, p = .135, η_P^2 = .103.

A main effect of orientation difference was found for hit rates with more large orientation difference targets detected as a proportion of the condition total (M = .95, SE = .01) compared to small (M = .92, SE = .01), *F*(1, 21) = 14.64, p = .001, η_P^2 = .411. An interaction between grasp congruency and orientation difference was also present for hit rates, *F*(1, 21) = 20.41, p < .001, η_P^2 = .493. Post-hoc t-tests revealed that for gratings with large orientation differences, hit rates were marginally higher when the gratings' orientation was congruent with the grasp cue (M = .95, SE = .007) compared to incongruent (M = .93, SE = .01), *t*(21) = 1.94, p = .066, however once corrected for multiple comparisons using Bonferroni adjustment this effect is not significant. No main effect of grasp congruency was found for false alarm rates, *F*(1, 21) = .08, p = .785, η_P^2 = .004 . For perceptual sensitivity (d'), a main effect of orientation difference was found with greater sensitivity for large differences (M = 2.58, SE = .07) compared to small (M = 1.85, SE = .04), *F*(1, 21) = 221.06, p < .001, η_{p2} = .913. No main effect of congruency or interaction with congruency was present for sensitivity (*F*(1, 21) = .001, p = .982, η_P^2 = .001, *F*(1, 21) = .99, p = .331, η_P^2 = .045, respectively).

Table 5. Accuracy and reaction times for Experiment 3 Chapter 5

	Difference	**Congruent**	**Incongruent**
Hits	**Small**	.93 (.05)	.92 (.05)
	Large	.95 (.03)	.93 (.05)
False alarms	**0°**	.19 (.09)	.19 (.07)
Sensitivity (d')	**Small**	1.83 (.34)	1.87 (.28)
	Large	2.60 (.44)	2.56 (.38)
Reaction times	**Small**	1179 (131)	1203 (150)
	Large	1154 (135)	1166 (139)

5.6. Discussion

Experiment 3 required participants to discriminate two spatial frequency gratings as the same or different in orientation, following a cue to prepare a grasping action, just as in Experiments 1 and 2. However, participants executed a pre-cued grasping action only when they perceived the stimuli to be different from each other in orientation, rather than the same. This simple change to the task instructions allowed for the measurement of the reaction time congruency effect as a function of difficulty in the task. While reaction times were affected by the difficulty of the discrimination, there was no interaction between grasp congruency and difficulty.

Given that the reaction times to the grating stimuli in Experiments 1-3 are gathered from the execution of the cued movement itself, it is possible that perception of the left/right oriented gratings facilitated the action, rather than the reverse. It seems unlikely that the reaction time effects observed here reflect *visual-motor,* rather than *motor-visual*, priming for a number of reasons. Firstly, participants are always cued to prepare the grasp in advance of the onset of the grating stimuli, so visual-motor priming would imply a strategy of inhibiting a movement cue that is highly informative, until after the onset of the grating stimuli. Nevertheless, it is possible that visual-motor priming contributes to some extent to the effects observed in Experiments 1-3. This alternative interpretation is directly addressed in the following Chapter 6, where the paradigm is adapted to a dual-task design. To anticipate those results, in line with previous motor-visual priming studies (e.g. see Exp. 4 & 5 in Craighero et al., 1999; also in Lindemann & Bekkering, 2009; Symes et al., 2008) the reaction time effects were maintained even when the effector used to signal the perceptual decision exhibits no congruency with the prepared action. This alternative interpretation of visual-motor priming can therefore be ruled out.

6. Chapter overview

Recent theories of action and perception suggest that bidirectional links exist between these two domains. Some reports have demonstrated that cueing a simple manual action can speed responses to stimuli that share a perceptual feature with the action (Craighero et al., 1999; Lindemann & Bekkering, 2009), suggesting visual processing is biased by prepared actions. However, speeded responses may reflect changes in early perceptual processing, or decision/response related processing. In three experiments the influence of planned actions on reaction times as well as perceptual sensitivity (*d'*) to discriminate visual stimuli that share a feature with the action was investigated. Participants discriminated the orientation of two spatial frequency gratings as the same or different in orientation. The difference between the gratings was continuously adjusted according to participants' performance throughout the task, in order to ensure the task acquired adequate error rates. The effect of cueing an oriented grasping action prior to stimulus onset was investigated across two levels of perceptual difficulty as well as two cue-target intervals.

In line with previous findings, we observed faster responses to stimuli that were oriented in the same direction as an oriented grasping action (Exp. 1-3). However, the accuracy and perceptual sensitivity (*d'*) to discriminate the stimuli were unaffected by the prepared action. This was true across two levels of discrimination difficulty that were continuously adapted to participants' performance across the task, as well as across two cue-target intervals (Exp. 2). Finally, the reaction time advantage observed for congruently oriented gratings was also unaffected by the difficulty of the discrimination (Exp. 3).

Chapter 6: AN ELECTROPHYSIOLOGICAL INVESTIGATION OF ACTION-MODULATED ORIENTATION PERCEPTION

1. Abstract

Previous research has shown that preparing actions speeds responses to action-relevant visual features, suggesting that how you *move* affects what you *see*. However, whether reaction time effects reflect an influence on early visual processing or not is unclear. Here, EEG was recorded during a task that combined perceptual discrimination and motor preparation. Participants were cued to prepare oriented reach-to-grasp actions before discriminating two spatial frequency gratings as the same or different. As expected, stimuli oriented in the same direction as the prepared grasp (congruent) were responded to faster than incongruently oriented stimuli. However, perceptual sensitivity (*d'*) to discriminate the stimuli was unaffected by action preparation. Furthermore, the observed reaction time effect was not reflected by modulations of early visual-evoked potentials. Instead beta-band (13-30Hz) synchronization over sensorimotor brain regions was influenced by the prepared action, indicative of improved response preparation. Together, these results suggest that reaction time effects of action on perception may not reflect modulations of early sensory processing. Instead, action preparation may influence higher order response or decision related processes in these tasks.

2. Introduction

Recent studies have shown that preparing simple grasping actions can influence performance on tasks of visual perception by speeding responses to stimuli with a feature consistent with the action, effects termed *motor-visual priming*. For example stimuli are responded to faster if they are oriented in the same direction as a manual grasping action (Craighero et al., 1999), if the stimuli's relative size is consistent with a prepared grasping action (Symes et al., 2008), or if the stimuli appear to rotate in the same direction as a manual object rotation (Lindemann & Bekkering, 2009). These effects suggest that mechanisms of action preparation are capable of influencing visual perception; in other words how you *move* may affect how you *see*. However, it is unclear whether faster responses to action-congruent stimuli indeed reflect biases in sensory perception, or in higher order decision or response related processes.

The fine temporal resolution of EEG is ideal for investigating effects of top-down priming of visual perception (e.g. see Mangun & Hillyard, 1991; Woodman, 2010). Studies have shown enhanced amplitudes of early event-related potential (ERP) components elicited by visual stimuli presented at attended areas of space (Hillyard, Vogel, & Luck, 1998; Hillyard & Anllo-Vento, 1998), at the goal location of eye-movements (Eimer et al., 2006a, 2007) as well as at effector and goal locations of reaching movements during reach preparation (Gherri et al., 2009; Job, de Fockert, & van Velzen, 2016; Mason et al., 2015). Furthermore, evidence now suggests that modulations of early ERP components also reflects the biasing of stimulus features, not just spatial locations (Karayanidis & Michie, 1997; Valdes-Sosa et al., 1998; Zhang & Luck, 2009). Despite the utility of this method, there have been surprisingly few EEG investigations of motor-visual priming. One exception (Wykowska & Schubö, 2012) combined visual search tasks for size or luminance targets with motor tasks of grasping and pointing while recording EEG. They observed that grasping (compared to pointing) facilitated visual search times for size targets, however this was not reflected by a modulation of early sensory ERP components. However, preparing a pointing action (compared to grasping) facilitated visual search times for luminance targets and this pattern was reflected by a modulation of an early (P1) event-related potential (ERP) component elicited by the target stimuli.

Here, EEG was recorded during a task combining perceptual discrimination and motor preparation in order to investigate the time course with which action affects perceptual processing. The motor-visual priming task used in Chapter 5 (Exp. 1) was adapted for this purpose. The task cued participants to prepare either a leftward or rightward oriented reach-to-grasp action on each trial. During the preparation of the action, participants were required to discriminate two spatial frequency gratings that could be oriented either leftward or rightward. On congruent trials (e.g. rightward oriented grasp with rightward oriented gratings), responses should be faster than on incongruent trials, as in the three experiments reported in Chapter 5. If the effect of grasping on stimulus processing reflects biases in early visual processing, then early ERP components (P1/N1) elicited by congruent targets should be enhanced relative to those elicited by incongruent targets.

Furthermore, cued motor preparation is typically accompanied by prominent changes in the power of beta oscillations (13-30 Hz) over central electrode sites (Cheyne, 2013; Kilavik et al., 2013; Pfurtscheller et al., 1996b). The source of these power changes is commonly attributed to the contralateral pre-Rolandic ‘sensorimotor’ region (Pfurtscheller & Berghold, 1989). While the exact functional role of beta band activity in cued movement tasks is not yet clear (see Kilavik et al., 2013 for a review), there is a general consensus that the dynamics of beta power provide a reliable indicator of the onset of motor preparation, execution as well as motor imagery (Kuhn et al., 2006; Pfurtscheller & Lopes da Silva, 1999; Pfurtscheller, Neuper, Flotzinger, & Pregenzer, 1997) and may reflect an active process promoting existing motor or cognitive states (Engel & Fries, 2010). Surprisingly, no motor-visual priming studies have investigated beta power. An exploratory approach was therefore taken to investigate whether action-congruency influences sensorimotor beta oscillations in the task.

As described in the discussion of Chapter 5, the prepared actions (left/right oriented grasps) in those experiments were signalled by the perceptual stimuli themselves. It is therefore possible that the effects reflect stimulus-response priming, rather than an effect of action planning on stimulus processing. In line with previous motor-visual priming studies (Craighero et al., 1999; Fagioli et al., 2007; Lindemann & Bekkering, 2009), if the effect does reflect motor-visual priming, then it should be observed for stimulus discriminations made with another response mode (e.g. key presses). Alternatively, if the perception of oriented stimuli primed congruent responses, no priming would occur for key presses, as they do not share a perceptual feature with the prepared action. Therefore, the paradigm from Chapter 5 was adapted to be dual-task, such that participants discriminate the grating stimuli with a key press response then subsequently execute the grasping action following a 'GO' stimulus. Chapter 2 (Experimental Methods) describes the advantages and disadvantages of single and dual-task designs in detail. If the reaction time advantage in response to congruently oriented grating observed in the Experiments 1-3 of Chapter 5 reflect motor-visual effects, rather than the reverse, then the effect should be present for key presses in this experiment. Additionally, as no interactions between discrimination difficulty and grasp congruency were observed for the experiments of Chapter 5 the factor of difficulty was removed from the design of this experiment.

3. Experiment 1

3.1. Participants

24 adults (18 females, mean ± SD of age: 27 years ± 4.32 years) participated in the experiment. All participants were right handed (mean laterality quotient (Veale, 2014) = 92.18, SD = 14.18) and reported normal or corrected to normal vision. The Local Ethics Committee at Goldsmiths, University of London, approved all experimental protocols and the experiment adhered to the ethical guidelines presented in the 1964 declaration of Helsinki. All participants provided written informed consent before the beginning of each experiment, and were debriefed at the end of the experiment as appropriate.

3.2. Stimuli & Task

The stimuli and task were identical to chapter 5 (Experiment 1), except for the following. The movement cues consisted of high (1000 Hz) and low (400 Hz) tones that were mapped to left or right grasping actions. The cue-tone mapping was counterbalanced across participants such that half of participants were instructed to prepare a leftward grasp following a high tone and the reverse instruction was given for the remaining participants. Participants were instructed to respond to the grating stimuli by pressing the ‘S’ or ‘D’ keys on a keyboard with the middle and the index finger of their left hand if they perceived the stimuli to be the same or different in orientation, respectively. Following this, a signal to execute the grasping movement was presented as the word ‘GO’ in the center of the screen. The largest orientation difference condition was removed so that the gratings could be identical to each other in their orientation (50% of trials) or different by a small degree (50% of trials). See Figure 13 for the trial procedure.

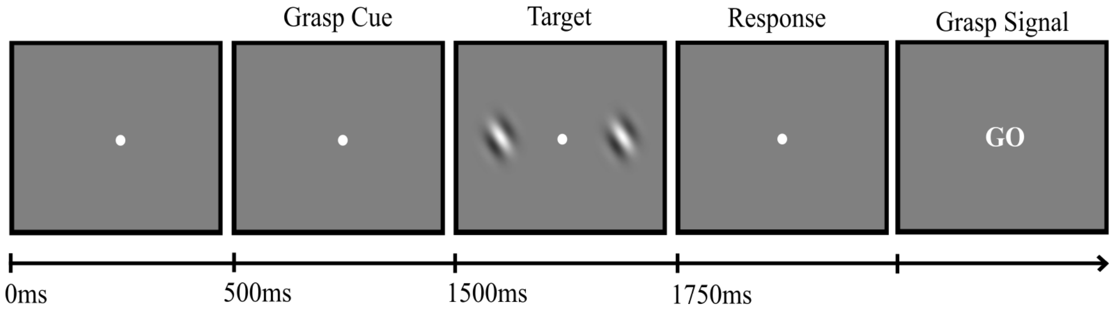

Figure 13. Trial procedure for Chapter 6: Experiment 1.
Participants are instructed to fixate on the central dot throughout the task. Grasp cues (1000Hz/400Hz tones) inform participants which grasp to prepare before spatial frequency gratings are presented. Participants then discriminate the gratings as the same or different in orientation from each other by pressing the 'S' or 'D' keys, respectively. A grasp signal ("GO") is presented 200ms after the key press, which signals the execution of the cued grasp.

3.3. Behavioural data analysis

Separate ANOVAs with grasp congruency (congruent/incongruent) as a within-subject factor were used to analyze the error rates, sensitivity values (d') and reaction times of the grating discrimination. For reaction time data, a mean of 3.65% (SD=.03) of trials were rejected for either having reaction times that fell outside ± 2.5 SD of the mean or because they corresponded to incorrect grasping.

3.4. EEG recording, processing & analysis

Chapter 2 outlines in detail the equipment and pipeline used to record and pre-processes the EEG data, therefore only a brief summary of the analysis is provided here.

For analysis of the stimulus evoked potentials, continuous EEG data were divided into 700ms epochs locked to the onset of the grating stimuli including a 100ms pre-stimulus baseline. Epochs including voltages exceeding + and/or - 100µV, well as epochs with discrimination or grasping errors, were automatically rejected prior to analysis. Eye-blink artefacts were corrected for using Independent Component Analysis (ICA). The mean amplitudes of ERP components within pre-defined time windows were extracted for analysis. The mean positive amplitude between 70 and 110ms post grating onset was extracted as the P1 mean amplitude. The mean of negative amplitudes between 130-170ms post grating onset was extracted as the N1 mean amplitude. Peak measures were extracted from electrode sites PO7 and PO8, which elicited the largest ERPs as observed in scalp maps of averages over all conditions. The difference between the mean P1 and N1 values was computed to obtain a mean peak-to-peak amplitude measure of the N1 component.

For the ERP analysis, the mean peak-to-peak amplitudes of the N1 component were analysed in a 2x2 repeated measures ANOVA with factors of grasp congruency (congruent/incongruent) and electrode hemisphere (PO7/PO8).

For analysis of beta power (13-30 Hz) following the grating stimuli, continuous EEG data were divided into 1000ms epochs including a 300ms pre-stimulus baseline. Time frequency representations of individual trials were then calculated using Morlet wavelet analysis with a wavelet width that linearly increased from 3 to 8 with the frequency range. The data was normalised to the pre-stimulus baseline period (-300ms to 0ms).

For statistical analysis of the stimulus-locked beta power, non-parametric cluster permutation (Maris & Oostenveld, 2007) was used. This approach to the analysis of multidimensional neuroimaging data extracts spatiotemporal regions showing significant differences between conditions or groups without any a priori assumptions of spatial regions or time windows. It therefore identifies effects that are robust within a cluster of electrodes/time points, rather than highly significant on one dimension (i.e. a single electrode and/or time point). The method is robust against Type I error as this is intrinsically controlled for by evaluating only the maximum cluster-level statistics under the null hypothesis.

The following steps were taken to identify significant clusters: 1) dependent samples t-statistics comparing grasp congruent and incongruent data were gathered for each of the samples in the multidimensional data structure; 2) t-statistics above a p-value threshold (p<.05) were then gathered; 3) Neighbouring data points exceeding the threshold were found; 4) The t-statistics were summed to calculate the cluster level statistic; 5) The maximum cluster statistic under its permutation distribution (shuffled data), derived from the test statistics obtained from the dependent samples t-tests based on 1000 random permutations, was evaluated. The cluster-level significance threshold was set at the two-tailed level of 0.025. Electrodes had an average of 6.6 neighbouring electrodes. Finally, dependent samples t-tests were run on beta values at cluster electrodes/time points comparing congruent and incongruent conditions.

3.5. Results

For reaction time data a main effect of grasp congruency was present, *F*(1, 23) = 8.16, p = .009, η_P^2 = .262, with faster responses to grating stimuli that were congruent with the cued grasp (822ms, SE = 21.31), compared to incongruent (842ms, SE = 20.85).

No effects of grasp congruency were present for hit rates (*F*(1, 23) = 3.02, p = .096, η_P^2 = .116), false alarm rates (*F*(1, 23) = .06, p = .803, η_P^2 = .003), or sensitivity (*F*(1, 23) = .15, p = .699, η_P^2 = .007).

Table 4. Accuracy and reaction times for Experiment 1 Chapter 6

	Congruent		**Incongruent**		**F-Ratio (1,23)**		
	M	**SD**	**M**	**SD**	**F-value**	**p-value**	η_P^2
Hit rate	.86	.07	.85	.08	3.02	.096	.116
False alarms	.14	.05	.14	.05	.06	.803	.003
Sensitivity (*d'*)	2.22	.27	2.19	.39	.15	.699	.007
Reaction times	822	104	842	102	8.16	.009	.262

Figure 14 shows the grand average event-related potentials (ERPs) elicited by grating stimuli. For the N1 mean peak-to-peak amplitude, no main effect of grasp congruency (*F*(1,23) = .05, p = .820, η_P^2 = .002), or electrode hemisphere (*F*(1,23) = .13, p = .717, η_P^2 = .006) was found nor an interaction between grasp congruency and electrode hemisphere (*F*(1,23) = .277, p = .604, η_P^2 = .012).[4]

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[4] Although Figure 14 shows a small difference between congruent and incongruent at the mean N1 component, rather than mean peak-to-peak N1 measure, this measure was similarly non-significant for the main effect of grasp congruency (*F*(1,23) = .04, p = .847, η_P^2 = .002).

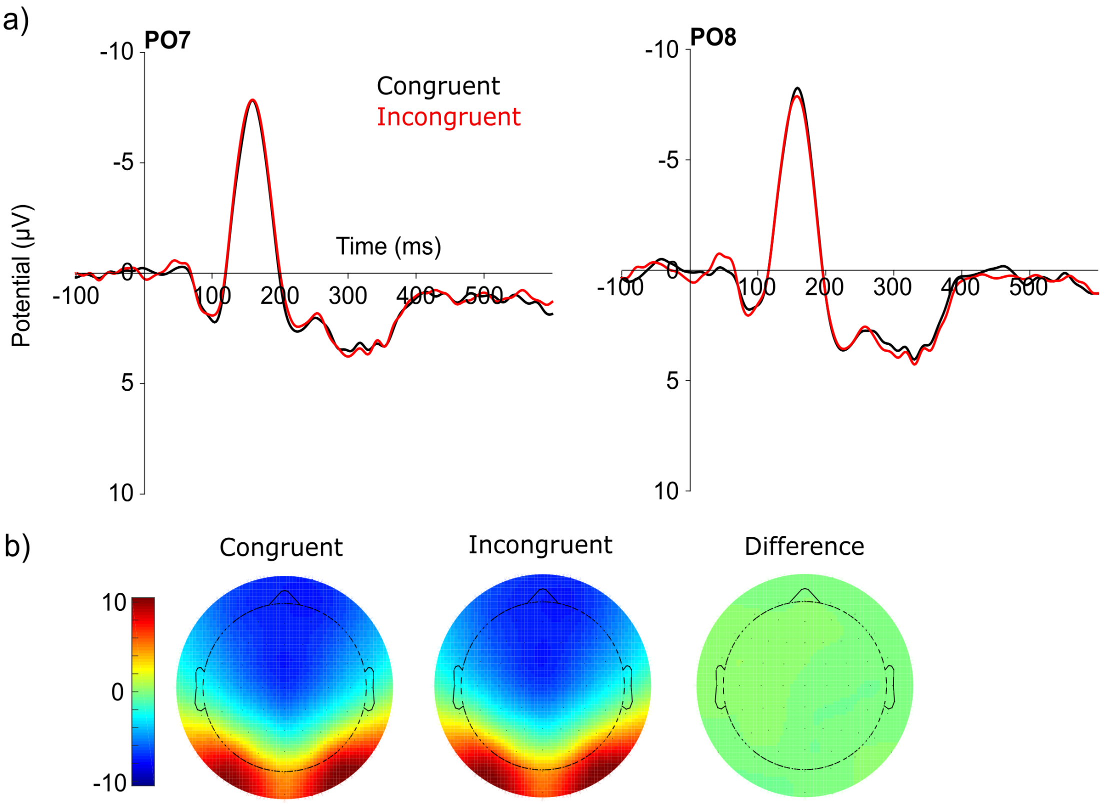

Figure 14. ERP results for Chapter 6: Experiment 1.
a) Grand average event-related potentials (ERPs) elicited by the grating stimuli (onset = 0ms) presented following cues to prepare congruently oriented (black) or incongruently oriented (red) reach-to-grasp actions. b) The scalp maps show the distribution of the N1 component peak-to-peak amplitude (µV) elicited by gratings presented following congruent grasp cues (left scalp map) and incongruent grasp cues (center scalp map) as well as the difference (right scalp map).

Time-frequency representations of the data were subjected to non-parametric cluster permutation (Maris & Oostenveld, 2007) in order to explore differences in beta band activity induced following grasp congruent and incongruent visual stimuli.

Figure 15 shows the power in the beta band (13-30Hz) following the grating stimuli that were oriented congruently or incongruently with the prepared grasping action. Higher beta power was observed in the congruent condition at left sensorimotor electrode sites (ipsilateral to the hand used to make the orientation discrimination key press). A significant positive cluster reflected this difference over sensorimotor electrode sites (significant cluster electrodes are highlighted, $p<.025$) from stimulus onset until approximately 200ms post-stimulus onset. A dependent samples t-test comparing mean beta power across cluster electrodes/time points for congruent and incongruent conditions showed that higher power (relative to baseline) was observed for the congruent (M = .97 SE = .03) compared to incongruent (M = .89, SE = .03) condition, *t*(23) = 3.12, p = .005.

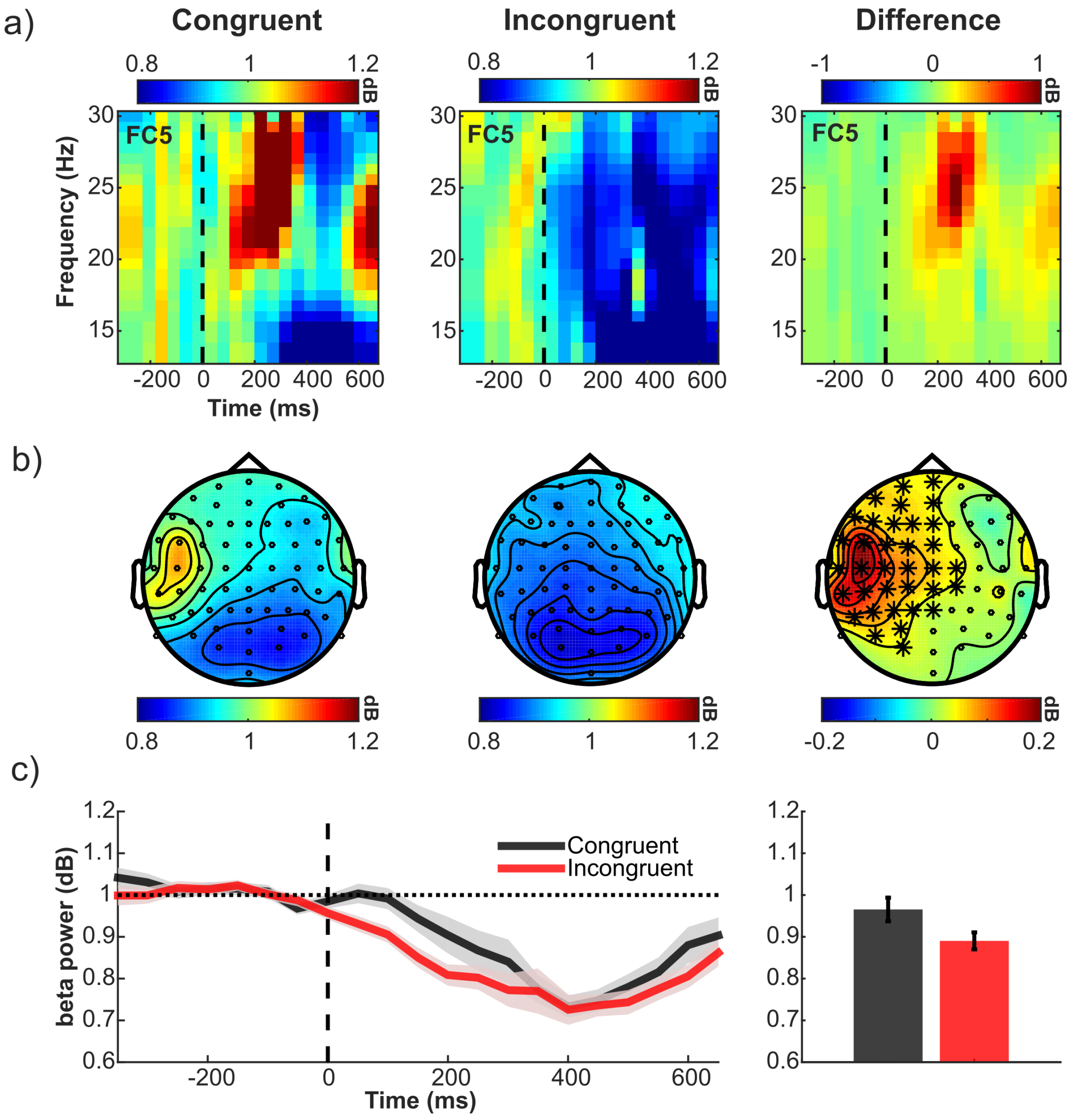

Figure 15. Beta synchrony results for Chapter 6: Experiment 1.
Grand averaged stimulus-locked power in the beta band (13-30Hz). a) Time-frequency plots at a representative electrode (FC5) locked to stimulus onset (dashed line). b) Scalp maps of beta power at significant time points. Significant cluster electrodes are highlighted. c) Beta power across time (left panel) averaged over significant cluster electrodes. Shaded areas show +/- SEM. The bar graph shows the averaged power at significant cluster electrode sites and time points for congruent (dark grey) and incongruent (red) conditions. Error bars show +/- SEM.

3.6. Discussion

The experiment had two key aims. Firstly, to further investigate whether the reaction time advantage for congruently oriented stimuli reflects changes in sensory perception. To do this, early event-related potentials elicited by the target stimuli during congruently or incongruently oriented grasping actions were compared. No differences in the amplitude of early ERPs evoked by the target stimuli were observed. We therefore do not find evidence that the reaction time advantage observed for the action-congruent stimulus feature is reflected by modulations in early visual processing.

Instead, greater power in the beta band (13-30Hz) was observed over sensorimotor electrode sites in the hemisphere ipsilateral to the hand used to make the orientation discrimination key press response. Modulations of power in the beta band over sensorimotor sites are commonly observed during the preparation of motor responses (Pfurtscheller & Lopes da Silva, 1999; Pfurtscheller & Neuper, 1997). Studies typically report event-related *desynchrony* (ERD) in the hemisphere contralateral to the hand used to execute the movement and event-related *synchrony* (ERS) in the hemisphere ipsilateral to the hand used. An increase in the amplitude of ERS is observed when the behaviour of large numbers of neurons synchronises (Pfurtscheller, Stancák, & Neuper, 1996a) and most likely requires coherent activity of cell assembles over at least several square centimetres (Lopes da Silva, 1991). When areas of neurons display such behaviour, active information processing is very unlikely and it can be assumed that the activity reflects a deactivated, or 'idling' state of the corresponding networks (Pfurtscheller & Lopes da Silva, 1999). This idea was supported by combined EEG/fMRI studies linking ERS/ERD to cerebral activation (Formaggio et al., 2008; Stevenson et al., 2011; Yuan et al., 2010). However, more recent theories propose that ERS instead reflects the maintenance of a current sensorimotor or cognitive state (Engel & Fries, 2010; cf Jenkinson & Brown, 2011), or even the dynamics of decision making processes (Spitzer & Haegens, 2017).

Increased beta power in the action-perception congruent condition may suggest that the left sensorimotor cortex underwent a greater suppression following a congruent, compared to incongruent imperative stimulus. This is consistent with the imperative stimulus requiring a left-hand key-press, hence right hemisphere dominance. Greater suppression of the left sensorimotor cortex (i.e. right hand) may result in speeded responses in the congruent condition, compared to the incongruent condition. Alternatively, the ERS of beta could reflect processing related to stimulus expectancy, in line with reports of ERS in the anticipation of stimuli requiring a motor response at and even before cue onset (Alegre et al., 2004; Fischer, Langner, Diers, Brocke, & Birbaumer, 2010; Molnár et al., 2008). This 'anticipatory' ERS is also absent in studies where the cue-target interval was variable, thus discouraging reliable temporal expectancy of the stimuli (Alegre et al., 2003; Doyle, Yarrow, & Brown, 2005). The beta ERS observed here, with a fixed cue-target interval, occurred around stimulus onset until approximately 200ms post onset, consistent with previous findings of anticipatory modulation of sensorimotor beta synchrony.

The second key aim was to rule out an alternative explanation of the findings of the experiments reported in Chapter 5 that the reaction time advantage reflected visual-motor rather than motor-visual priming. To do this, the paradigm was adapted into a dual-task such that the orientation discrimination was made using a response mode that did not contain a congruency with pre-cued action (key press) and the pre-cued action was instead signalled by a subsequent neutral 'GO' stimulus. The reaction time advantage of congruently oriented targets was again observed in this experiment. This rules out the alternative interpretation of the experiments reported in Chapter 5. The effects observed in Chapter 5 therefore indeed reflect motor-visual priming rather than visual-motor priming. This is in line with many previous motor-visual priming studies whereby reaction time effects were maintained even when the effector used to signal the perceptual decision exhibits no congruency with the prepared action (e.g. see Exp. 4 & 5 in Craighero et al., 1999; Lindemann & Bekkering, 2009; Symes et al., 2008).

Chapter 7: GENERAL DISCUSSION

The experiments reported in this thesis investigate the coupling between action and perception, specifically regarding how processes of visual perception are altered during action preparation. Current theoretical frameworks such as the Premotor Theory of Attention (Rizzolatti & Craighero, 1998; Rizzolatti et al., 1994) and common coding approaches such as the Theory of Event Coding (TEC, Hommel et al., 2001) propose a tight and bidirectional coupling between processes of action planning and visual perception. Indeed, in order to successfully plan and execute even the simplest of movements, perceptual and motor processes need to work in concert. For example, before one can reach out and grasp an object, sensory information about the object must feed into the movement plan and sensorimotor transformations must be carried out. To achieve this, recent theories propose that processes of perceiving objects and acting upon them share a representational domain in the brain. This is in stark contrast to the classical understanding of perception and action systems as structurally and functionally independent of each other.

Empirical evidence for a tight coupling between perception and action has sought to demonstrate bidirectional links between processes of perceiving and acting upon stimulus features. While it is well known that perceiving objects can trigger their associated motor behaviours, the reverse effect has also been observed such that preparing a simple movement can prime action-relevant stimulus features. The focus of this thesis is the latter effect, commonly referred to as *motor-visual priming*.

The mechanisms underlying effects of action on perception are poorly understood, particularly regarding how exactly action preparation exerts an influence on non-spatial visual processing. The aforementioned theoretical models predict that incoming sensory perceptual processing should be influenced by a prepared action, however despite this clear prediction very few investigations have addressed the stage at which visual processing is influenced by action preparation. The core aims of this thesis are to further the evidence for effects of action preparation on visual perception and to investigate the underlying mechanisms of such effects. This chapter provides a discussion of the empirical findings reported in this thesis and their relevance for our understanding of perception-action coupling.

1. Selection-for-action

The selection of relevant information is a necessary requirement for successfully perceiving and interacting with the external world. In Chapter 1 *selection-for-action* was introduced as the theoretical framework that challenged assumptions about why and how information from the environment is selected. Early proponents such as Allport (Allport, 1987) and Neumann (Neumann, 1990) appreciated that the selection of information from our environment not only serves a goal of enhancing the *perception* of objects (selection-for-perception), but ultimately serves the goal of successfully acting upon those objects (selection-for-action). In other words, selecting action-relevant sensory information from the environment is crucial to successfully produce adaptive motor behaviours. The selection-for-action approach therefore ultimately challenges notions of a strict separation between perceptual and action systems and proposes that mechanisms of selection must be at work while producing actions.

In parallel to the development of the selection-for-action approach, research also began to reveal a role of action in the mechanisms of selective attention. The premotor theory of attention (Craighero & Rizzolatti, 2005; Rizzolatti et al., 1987) proposed a tight coupling between perception and action in the form of shared control mechanisms of attention and action. According to the premotor theory, the brain circuitry responsible for the coding of spatial representations is also responsible for coding motor programs. The theory therefore asserts that shifts in spatial attention occur as weaker activations of the same neural circuity that control movements.

Another explanatory framework for the links between action and perception is known as the theory of event coding (TEC, Hommel et al., 2001). TEC is rooted in much earlier ideas that imagined actions tend to evoke the execution of those actions, broadly referred to as *ideomotor* interactions (James, 1890; Lotze, 1852). TEC asserts that actions are represented in terms of their sensory effects and that 'imagined' or 'prepared' actions therefore evoke representations of the perceptual objects associated with those actions. Both the premotor theory of attention and TEC predict bidirectional links between perception and action, such that perceiving objects should influence motor behaviours and the reverse; preparing motor behaviours should influence perception of object features. However, the premotor theory, being more rooted in neurophysiology, makes clearer predictions about the neural mechanisms underlying the links between attentional selection of sensory information and action planning.

Much of the evidence for the premotor theory has demonstrated a remarkable similarity between effects of shifting attention to a location in space and preparing to move towards that area of space. For example, extensive studies have demonstrated that stimuli receive preferential processing if they appear at the location of an upcoming eye-movement (Deubel & Schneider, 1996a; Hoffman & Subramaniam, 1995; Shepherd et al., 1986) as well as at the goal location of an upcoming reaching or pointing movement (Deubel et al., 1998). These behavioural findings have been corroborated by neuroimaging studies showing a remarkable overlap in the brain areas activated during tasks of visual-spatial attention and simple movements (Astafiev et al., 2003; Maurizio Corbetta, 1998; Perry & Zeki, 2000).

The premotor theory has been extended from explaining the orienting of attention to spatial locations to the orienting of attention to objects. Studies on non-human primates showed that many neurons located in the monkey anterior intraparietal sulcus (AIP) and premotor cortex (F5) would selectively discharge both when grasping an object and when viewing a graspable object (Rizzolatti & Luppino, 2001). Importantly, these neurons would only discharge when the properties of the object (size and shape) matched the grasping action (precision or power grasping). This suggests that the shared control mechanisms between attention and action are not limited to spatial processing, but also the processing of non-spatial object features.

2. Action planning and the perception of non-spatial features

The experiments reported in this thesis investigate the neural mechanisms underlying effects of action preparation on visual perception of non-spatial features. This was addressed using both behavioural and electrophysiological measures of visual perception during the planning phase of grasping actions.

The empirical evidence for a tight coupling between perception and action initially focused on the spatial domain, with findings demonstrating effects of action preparation on perceptual processing across action-(ir)relevant spatial locations. Early findings showed that stimuli received preferential processing if they appeared at the goal location of a planned eye-movement, compared to a non-goal location (Deubel & Schneider, 1996b; Hoffman & Subramaniam, 1995; Shepherd et al., 1986). These findings likened effects of planned eye-movements on visual processing to effects of shifting covert spatial attention. More recently the premotor theory was also extended from explaining the orienting of attention to spatial locations to the orienting of attention to objects. Studies on non-human primates have shown that many neurons located in the monkey anterior intraparietal area (AIP) and premotor cortex (F5) would selectively discharge both when grasping an object and when viewing a graspable object (Rizzolatti & Luppino, 2001). Crucially, these neurons would only discharge when the properties of the object (size and shape) were congruent with the grasping action (precision and whole hand power grasping). This suggests that actions do not only result in an orienting towards action-relevant spatial locations, but also non-spatial object features.

The behavioural findings from this thesis broadly support the more recent extension of the premotor theory of attention to include non-spatial visual processing. Across the experiments reported here, the processing of non-spatial stimulus features was investigated during the preparation of different types of grasping actions. Local/global processing was investigated in Chapters 3 and 4, stimulus size was investigated in Chapter 4, and stimulus orientation was investigated in Chapters 5 and 6. A brief overview of the behavioural findings is provided next.

The findings provided in Chapter 3 and 4 are the first to show an influence of different versions of the same basic action, power and precision grasps, on visual perception of hierarchical information. Experiment 1 demonstrated that the preparation of either small or large grasping actions modulates reaction times to local targets presented in compound stimuli. Faster reaction times were observed for targets presented at the local level of compound stimuli with a precision grasp, relative to a power grasp. Experiment 2 manipulated the relative saliency of the global level by using fewer local elements in the compound stimuli and observed the same influence of grasp cueing on reaction times for local targets, for right hand responses. This shows that the effect of action preparation is not dependent on the commonly observed global bias.

The findings provided in Chapters 5 and 6 showed a robust effect of planning an oriented reach-to-grasp action on the speed of discriminating two oriented grating stimuli as the same or different. Crucially, the overall orientation of the two gratings (leftward or rightward) could be congruent or incongruent with the prepared grasping action (leftward or rightward). Across all four experiments, faster reaction times to discriminate congruently oriented stimuli, compared to incongruently oriented stimuli, were observed. This effect of priming was unaffected by the length of the cue-target interval, the difficulty of the perceptual discrimination as well as the target response instruction (i.e. targets defined as 'same' or 'different' gratings).

Together, this supports the extension of the pre-motor theory of attention to include non-spatial features. While the premotor theory originally focused on the importance of 'spatial maps' in the parietal cortex for the control of attention, more recent evidence therefore suggests that non-spatial feature representations may be similarly coupled to motor programming. This notion is also in line with common coding approaches such as TEC, although TEC remains more focused on selection at the level of feature dimensions, for example selecting information based on a feature dimension like colour, while ignoring another feature dimension such as orientation. Here the focus is on the prioritisation of specific features, within a feature dimension.

In line with the view that action and object perception are tightly coupled, extensive research has shown that simply viewing objects can potentiate actions associated with those objects (Symes et al., 2005; Tucker & Ellis, 1998). Studies initially focused on spatial relationships between presented objects and actions. For example, in Tucker and Ellis's (1998) seminal study, participants were presented with images of graspable objects and asked to respond with the left or right hand if the images were upright or inverted. Reaction times were faster when the hand used to make the response was most suited to grasp the presented object. Subsequent studies identified non-spatial effects in which power and precision grasp responses were primed by the task-irrelevant size of everyday objects (Ellis & Tucker, 2000; Tucker & Ellis, 2001). Broadly, these findings suggest that the representation of objects to some extent includes processing of the actions with which those objects are associated with, otherwise known as their *object affordances*. The motor-visual priming effects presented in this thesis and the object affordance effects previously described can be thought of two sides of the same coin. Both seek to investigate the tight coupling between action and perception, albeit by demonstrating opposite effects. Object affordance effects have shown that grasping actions can be primed by the presentation of graspable objects, suggesting that object perception entails some form of motor processing. On the other hand, the motor-visual priming effects reported here show that the processing of visual features can be primed by prepared actions, suggesting that action planning evokes visual representations of action-relevant features.

3. Modulations of early ERP components across the experiments

While the reaction time effects observed across the experiments reported in this thesis are mostly consistent, showing faster reaction times for action-congruent stimuli, the ERP findings do not share this consistency. Early ERPs elicited by action-congruent stimuli were enhanced in Chapter 4, such that larger stimuli elicited enhanced N1 component amplitudes during power grasp preparation, compared to precision grasp preparation and the reverse effect was observed for smaller stimuli. However, no such modulation was observed in Chapter 6 for congruently oriented grating stimuli. Interpreting this inconsistency is made difficult by the large number of differences between the experiments. Not only were different grasping actions cued across the tasks (power/precision grasps in Chapter 4 and leftward/rightward reach-to-grasp actions in chapter 6), but different perceptual features were also investigated (size in Chapter 4 and orientation in Chapter 6). However, it is unclear why only size, but not orientation would be modulated by power/precision grasping, but not oriented grasping. Indeed, none of the dominant models of action-modulated cognition predict that only certain action-relevant features should be influenced by certain action types. Although speculative, some potential explanations for the disparate ERP findings are explored next.

One entirely plausible explanation is that action preparation does indeed exert an influence on early visual processing of orientation in Chapter 6, eventually resulting in the faster reaction times to congruently oriented stimuli. However, this influence may not be reflected by modulations of early visual-evoked potentials, resulting in the lack of a difference in amplitude across conditions. It is conceivable that early visual processing is in fact modulated by action preparation in that task, but this is either not measurable with EEG or is perhaps removed and/or concealed by the averaging process necessary to garner ERP waveforms. In the Experimental Methods chapter the limited conclusions that can be drawn from the ERP methodology are outlined in more detail.

Why were early ERP components modulated by action preparation in the experiment reported in Chapter 4, but not chapter 6, given that the same underlying mechanism were predicted? One of the most notable differences between the designs of the experiments reported in Chapters 4 and 6 is the task-relevance of the perceptual stimulus. The stimuli used in Chapter 4 were wholly irrelevant stimuli, requiring no response. However, in Chapter 6 participants were required to respond to the stimuli by discriminating whether they were identical or not. Much of the evidence for early modulations of visual ERPs during action preparation has used wholly task-irrelevant stimuli. This technique is often referred to as a 'dot-probe' paradigm in which sensory processing is 'probed' by briefly flashing a task-irrelevant visual stimulus to measure the early visually-evoked potentials elicited by the stimulus. The brain's early response to exactly the same stimulus is reliably modulated by preparing an action, such that enhanced P1 and N1 component amplitudes are observed when a movement is prepared towards that location, compared to another location. This technique is primarily used to reveal covert shifts in visual-spatial processing during movement preparation, although similar effects have been shown in tasks of feature detection (Luck, Fan, & Hillyard, 1993). However, the grating stimuli in Chapter 6 were not primarily used as 'task-irrelevant probes', because they also required a behavioural response. It is conceivable that the requirement for a response could discourage early sensory selection until a later stage downstream of sensory perception, resulting in no differences in the early ERP components elicited by the stimuli. The question of how the wider context of the task influences modulations of early sensory ERP components is an intriguing one. Indeed some findings have shown that simply changing the task instructions to emphasis either the goal location of a movement or the effector to be used can alter the pattern of early ERP component effects (Gherri et al., 2009). Such findings suggest that effects of action on sensory processing may be dependent on a range of contextual factors. Actions rarely occur in isolation, and the ways in which aspects of the surrounding context, including task-demands, behavioural goals as well as practice and familiarity, affect action-perception coupling remains a key area of investigation. Further research on these contextual factors could help to reveal a certain flexibility in these mechanism, perhaps tailored to the current setting.

4. Sensory gain as a mechanism of action-modulated visual processing?

The mechanisms underlying attentional selection are most often attributed to an amplification, or gain increase, in the neural populations coding for an attended stimulus (for a review see Hillyard et al., 1998). This 'sensory gain' account views attention as operating at the level of sensory perception, such that when a feature is attended to, the firing rate of neural populations processing those features is increased (Hillyard & Anllo-Vento, 1998). A wide variety of evidence supports the sensory gain account of attention. For example, attending to a certain attribute of a stimulus (shape, colour or velocity) not only increases sensitivity to discriminate the stimulus, compared to dividing attention between those attributes, but this also enhances the neural activity of different regions specialized for processing information related to the selected attribute (Corbetta, Miezin, Dobmeyer, Shulman, & Petersen, 1990). This suggests that attention operates by enhancing sensory processing in the same areas that are coding for the stimulus when it is unattended, rather existing as a structurally independent entity in the brain. Furthermore, electrophysiological responses elicited by task-irrelevant visual stimuli presented at attended, compared to unattended, locations are enhanced at very early sensory stages of visual processing (for reviews see Hillyard et al., 1998; Hillyard & Anllo-Vento, 1998).

Sensory gain mechanisms have also been attributed to effects of action preparation on perception, given the known links between attention and action preparation, made explicit in the aforementioned premotor theory of attention (Craighero & Rizzolatti, 2005; Rizzolatti et al., 1987). There is now extensive evidence that sensory gain mechanisms may also underpin effects of preparing spatially guided movements on visual perception. Many studies have shown that early ERP components elicited by task-irrelevant visual stimuli are enhanced also when participants are preparing to move toward the location of the stimulus, compared to another location. Studies have shown that preparing a variety of spatially guided movements (eye-movements, reaching, pointing and grasping) results in modulations of early ERP components (P1/N1) known to index sensory processing in extrastriate visual cortex. For example, P1 and N1 components elicited by task-irrelevant visual stimuli are enhanced if they appear at the goal location of planned eye-movements (Eimer, Van Velzen, Gherri, & Press, 2006b; Eimer et al., 2007), as well as at effector and goal locations of reaching movements (Gherri et al., 2009; Job et al., 2016; Mason et al., 2015). This suggests a similar gain in sensory processing at spatial locations that are not only the locus of visual attention but are areas that are relevant to an upcoming action.

While many findings support a sensory gain account during action preparation at spatial locations relevant for the movement, whether the same mechanisms operate to facilitate non-spatial stimulus features is poorly understood. Very few studies have investigated early sensory processing of non-spatial stimulus features in the context of action preparation. One exception (Wykowska & Schubö, 2012) combined visual search tasks for size or luminance targets with motor tasks of grasping and pointing while recording EEG. The P1 component elicited by luminance targets was enhanced during the planning phase of a pointing movement, compared to a grasping movement. While the authors also predicted the reverse effect for the size targets (i.e. enhanced early ERP component amplitudes while preparing a grasping, compared to pointing action), no such effect was observed. It is unclear why sensory perception of luminance, but not size, would be modulated by action preparation in their task and indeed the sensory gain account cannot easily account for such a pattern of results.

The results of Chapters 5 and 6 of this thesis are also not easily explained by a sensory gain account of action-modulated visual processing. In these experiments a robust behavioural effect of action preparation on a task of visual perception was observed, such that preparing an oriented reach-to-grasp action decreased reaction times to discriminate stimuli that were oriented in the same direction as the prepared grasping action, compared to stimuli oriented in the opposite direction. However, in all four experiments, sensitivity to discriminate the stimuli was unaffected by the congruency of the prepared action, and furthermore in Chapter 6 – Experiment 1, the amplitude of early ERP components was unaffected by action preparation. Instead synchronization of beta oscillations (13-30 Hz) was observed over sensorimotor areas, indicative of improved motor preparation following congruently oriented stimuli. Together, this suggests that the reaction time advantage for action-congruent stimuli may not reflect a gain in the sensory processing of those stimuli. Instead action preparation likely influenced later stages of information processing beyond early sensory processing.

The studies reported in Chapters 5 and 6 are not the only ones to report null effects of action on behavioural tasks of perceptual accuracy. Another previous study reported three experiments in which left/right pointing movements were cued and accuracy to discriminate a visual target that appeared at the goal of the movement or at a different location was measured (Bonfiglioli, Duncan, Rorden, & Kennett, 2002). They found that the perceptual report was unaffected by the direction of the prepared action, across four different stimulus-onset-asynchronies. These inconsistencies in the available literature highlight that the circumstances in which action can exert an effect on tasks of visual perception are clearly not as simple as the current models suggest. One possibly overlooked factor could be the temporal structure of the tasks used and a lack of appreciation that effects of action on perception are likely highly dynamic and temporally specific. This issue is discussed in more detail next.

5. When does action influence perception?

The majority of the experiments reported in this thesis presented the visual stimulus at a fixed interval of 1000ms after the onset of the movement cue. This interval, or close to it, has been used in many tasks investigating visual processing during action planning. However, it is of course possible that effects of action preparation on perception may be temporally dynamic, continually adjusting the weights of different sensory inputs across time.

In Chapter 5 (Experiment 2), the time interval length between the movement cue and the visual stimulus was halved such that the visual stimulus was presented 500ms after the onset of the movement cue, rather than 100ms. In that experiment the timing of the stimulus presentation did little to influence the effect of action preparation on discriminating the visual stimuli. Although this was a very coarse investigation of the temporal profile of motor-visual priming, with just two time points, it nevertheless suggests rather consistent performance of visual discrimination across the time course of movement preparation.

All of the experiments reported in this thesis have used variations of a basic 'delayed movement paradigm', in which participants are cued to prepare a movement but told to withhold execution of the movement until an imperative 'GO' stimulus is presented. Visual perception is then probed during the delay, in which it is assumed that the action is prepared. However, some studies adopt a slightly different approach in which participants are instructed to execute the movement as soon as they are presented with the cue. In these 'immediate movement' paradigms, movement preparation is defined as the interval between cue onset and movement initiation, rather than cue onset and GO stimulus onset. Studies using immediate movement paradigms have identified a temporally dynamic influence of action on perception. For example, almost immediately before the onset of an eye-movement (~100ms before eye-movement onset), the processing of basic features such as orientation, colour and spatial frequency is improved at the landing point of the eye-movement (Li, Barbot, & Carrasco, 2016; Rolfs & Carrasco, 2012). Importantly, these effects also appear to increase closer in time to the onset of the movement. Similar behavioural effects are also observed at the goal location of reaching movements (Rolfs, Lawrence, & Carrasco, 2013). Furthermore, another recent study measured ERPs in response to task-irrelevant visual stimuli presented in the interval just after the onset of a GO stimulus signaling a reaching movement, but before participants had executed the movement (Mason et al., 2015). Early sensory ERP component amplitudes were enhanced at the goal location of the reaching movements during that interval. To date, no studies have investigated perceptual processing during grasp preparation at this time interval (i.e. just before and approaching movement onset). Instead most studies, including those presented in this thesis, deliver the visual stimulus at a fixed interval after onset of the cue, rather than relative to movement onset. How exactly effects of action on perception may differ between delayed movement tasks and immediate movement tasks is so far unknown. A systematic investigation of the temporal profile of perceptual processing across action preparation starting from the onset of the movement cue until movement initiation would be extremely informative. In particular, using a psychophysics approach, detection and/or discrimination thresholds of action-(in)congruent visual stimuli presented across a large number of temporal onsets could provide a more precise estimation of action-modulated perceptual processing.

6. The difficulty of the perceptual task

Across the three experiments reported in Chapter 5, the difficulty of the perceptual discrimination had a large effect on reaction times, accuracy, and sensitivity (*d'*), such that responses were faster and more accurate for larger orientation differences (easy to discriminate) versus small orientation differences (difficult to discriminate). However, the effect of grasp congruency was unaffected by the difficulty of the perceptual discrimination. This suggests that any coupling between perception and action observed here is not affected by the difficulty of the perceptual discrimination. This is in contrast to evidence that increasing the number of items in visual search tasks influences motor-visual priming effects (Bekkering & Neggers, 2002; Hannus et al., 2005) with effects vanishing at larger set sizes. This initially suggested that the processing resources shared by action and perception are to some extent capacity limited, as at larger set sizes there are insufficient resources for actions to further enhance stimulus processing. However, in Bekkering and Neggers' (2002) study, motor-visual priming also disappeared at very low set sizes, suggesting that behaviorally relevant stimuli are facilitated only when the task is not too difficult, but also not too easy. Furthermore in line with our findings Gutteling and colleagues (2011) also found, across three levels of difficulty, similar effects of preparing a grasping (versus pointing) action on orientation change detection. Overall there is therefore no strong evidence that effects of action on perception are limited by the capacity of perceptual resources.

APPENDICES

1. Pilot Phase

1.1. Pilot Study 1: Concurrent bimanual grasping

The relationship between local/global processing and precision/power grasping was investigating using a task that combined local/global target detection with concurrent precision/power grasping. On each trial, participants (n=12) were required to detect a target shape that could appear at either the local or the global level of a hierarchical stimulus or could be absent from the display. Vocal reaction times were recorded in response to the target stimuli. In alternating blocks, participants were instructed to hold and squeeze with both hands either two power, or two precision, grasping devices. Both the stimuli and power/precision grasping devices used were identical to those used in Experiment 1 (Chapter 3). Reaction times to targets appearing at the global and local level, as well as during concurrent power and precision grasping were compared using a repeated measures two-way ANOVA with factors of target level (global vs. local) and grasp type (power vs. precision).

Table 5 (1st panel) shows the mean reaction times and standard deviations for each condition. A significant main effect of target level was observed (*F*(1, 11) = 5.84, p = .034, η_P^2 = .347) with faster responses to global (M = 459, SE = 17.5), compared to local (M = 476, SE = 14.9), targets by 17ms (SE = 7.16). No significant effect of grasp type was observed (*F*(1, 11) = .35, p = .566, η_P^2 = .031) or interaction between the factors of level and grasp type (*F*(1, 11) = .07, p = .798, η_P^2 = .006). This suggests that local/global processing is unaffected by simply executing either precision or power grasping actions concurrently.

1.2. *Pilot Study 2: Offline unimanual grasping*

Pilot 2 investigated whether performing the action *offline* influences subsequent local/global processing. The local/global target detection task was identical to Experiment 1 Chapter 3, where participants (n=11) were required to detect a target shape that could appear at either the local or the global level of a hierarchical stimulus or could be absent from the display. Prior to each block of local/global target detection, participants were instructed to hold and grasp either a power or precision grasping device with their right or left hand until instructed otherwise (grasp duration of 2 mins). Following each block of grasping participants completed a block of the local/global target detection task. Six blocks alternated between grasp type, the order of which was counterbalanced across subjects. Vocal reaction times were compared using a repeated measures ANOVA with factors of target level (global vs. local), grasp (power vs. precision) and hand used (right vs. left).

A significant main effect of target level was observed ($F(1, 10) = 15.58$, $p = .003$, $\eta_P^2 = .609$) with faster reaction times to Global targets (M = 435, SE = 14.53) compared to Local targets (M = 452, SE = 13.75) by 17ms (SE = 4.10). No significant effect of grasp type was observed ($F(1, 10) = .102$, $p = .756$, $\eta_P^2 = .010$), or hand used ($F(1, 10) = 2.46$, $p = .148$, $\eta_P^2 = .197$). No significant interactions were observed (all p-values > .05). This suggests that performing a precision or power grasping action offline is not sufficient to prime the processing of local global stimulus features.

1.3. *Pilot Study 3: Unimanual Grasping vs. Pointing*

Pilot 3 investigated whether planning to make a grasping, compared to pointing, action influences the detection of local/global target stimuli. In a motor-visual priming paradigm, participants (n=10) were required to detect a target shape that could appear at either the local or the global level of a hierarchical stimulus or could be absent from the display. Each trial was initiated when the participant rested their hand over a lever device. After 500ms a centrally presented fixation cross changed colour to blue or green, which cued participants to prepare a grasping or a pointing action. Participants withheld execution of the action for 1000ms until the presentation of a target shape stimulus. The target could appear at either the local or the global level of a compound stimulus or be absent from the display. Once the target had been detected, participants released their hand from the lever device, which registered a reaction time, and executed the prepared reached-to-grasp or reach-to-point action on a second device placed below the display as fast as possible. To make the pointing action participants touched a small microswitch button with their index finger, which registered a response. To make the grasping action participants used their whole hand to grasp and pick up the device, which released a micro-switch lever on the underneath of the device. Figure 16 shows the experimental setup for Pilot study 3.

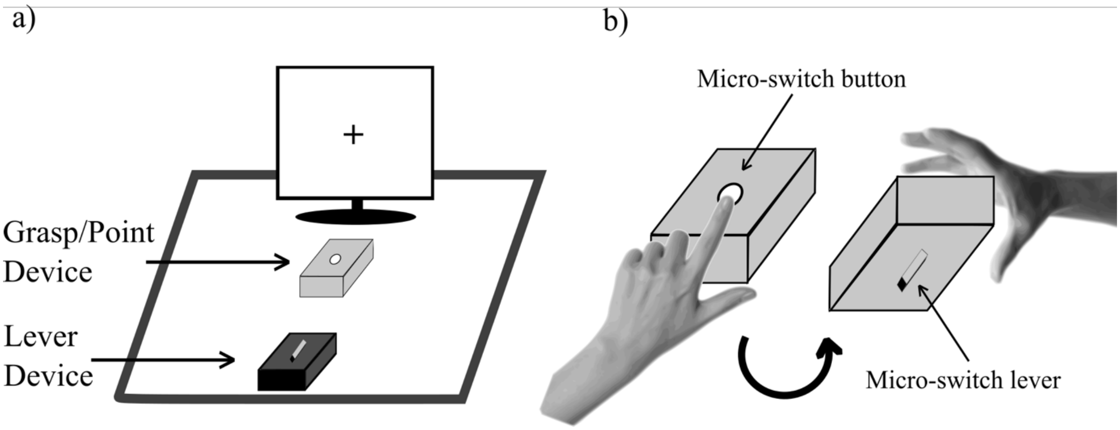

Figure 16. Experimental set-up for pilot study 3.
a) Pressing and holding a lever device initiated each trial. The colour of the fixation cross (blue or green) instructed participants to prepare either a pointing or reaching action toward the light grey device. b) The device used to afford either a pointing or grasping action. The pointing action required participants to release their hand from the lever device and touch the micro-switch button with their index finger only. The grasping action required participants to use their whole hand to grasp and lift the device, which released a micro-switch lever on the underneath of the device.

Table 5 (4th panel) shows the mean reaction times and standard deviations for each condition. A significant main effect of movement type was observed (*F*(1, 9) = 12.97, p = .006,) η_P^2 = .590 with faster responses using a grasping action (M = 547, SE = 37.88) compared to a pointing action (M = 560, SE = 36.76) by 13ms (SE = 3.62). No other main effects or interactions were significant (all p-values > .05). This suggests that target detection was faster when a grasping action was planned, compared to a pointing action. However, the movement type (grasping vs. pointing) did not interact with the target level (local vs. global). It is unclear whether participants were simply faster at planning grasping vs. pointing actions, or whether target detection was factilitated by the planning of a grasping, compared to pointing action.

Table 5. Reaction times and standard deviations for Pilot studies 1-3

		Global Target		**Local Target**	
Pilot 1	**Power**	461 (65)		480 (55)	
	Precision	457 (60)		474 (53)	
		Right Hand	**Left Hand**	**Right Hand**	**Left Hand**
Pilot 2	**Power**	438 (50)	435 (59)	454 (44)	455 (48)
	Precision	444 (57)	427 (50)	547 (59)	443 (49)
Pilot 3	**Grasp**	551 (123)	544 (132)	550 (117)	545 (117)
	Point	563 (129)	547 (109)	573 (119)	558 (118)

2. Edinburgh Handedness Inventory

Edinburgh Handedness Inventory

Surname__________________________Given Name___________________________

Date of Birth_____________________________Sex____________________________

Please indicate your preferences in the use of hands in the following activities by *putting + in the appropriate column*. Where the preference is so strong that you would never try to use the other hand unless absolutely forced to, *put ++*. If any case you are really indifferent put + in both columns.

Some of the activities require both hands. In these cases the part of the task, or object, for which hand preference is wanted is indicated in brackets.

Please try to answer all the questions, and only leave a blank if you have no experience at all of the object or task.

	Left	Right
1. Writing		
2. Drawing		
3. Throwing		
4. Scissors		
5. Toothbrush		
6. Knife (without fork)		
7. Spoon		
8. Broom (upper hand)		
9. Striking Match (match)		
10. Opening box (lid)		
i. Which foot do you prefer to kick with?		
ii. Which eye do you use when using only one?		

L.Q.	Leave the spaces blank	DECLE

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