INFLUENCE OF GAZE POSITION ON GRASP PARAMETERS FOR REACHES TO VISIBLE AND REMEMBERED STIMULI

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ABSTRACT

In order to pick up or manipulate a seen object, one must use visual signals to aim and transport the hand to the object's location (reach), and configure the digits to the shape of the object (grasp). It has been shown that reach and grasp are controlled by separate neural pathways. In real world conditions, however, all of these signals (gaze, reach, grasp) must interact to provide accurate eye-hand coordination. The interactions between gaze, reach, and grasp parameters have not been comprehensively studied in humans. The purpose of the study was to investigate 1) the effect of gaze and target positions on grasp location, amplitude, and orientation, and 2) the influence of visual feedback of the hand and target on the final grasp components and on the spatial deviations associated with gaze direction and target position. Seven subjects reached to grasp a rectangular "virtual" target presented at three orientations, three locations, and with three gaze fixation positions during open- and closed-loop conditions. Participants showed gaze- and target-dependent deviations in grasp parameters that could not be predicted from previous studies. Our results showed that both reach- and grasp-related deviations were affected by stimulus position. The interaction effects of gaze and reach position revealed complex mechanisms, and their impacts were different in each grasp parameter. The impacts of gaze direction on grasp deviation were dependent on target position in space, especially for grasp location and amplitude. Gaze direction had little impact on grasp orientation. Visual feedback about the hand and target modulated the reach- and gaze- related impacts. The results suggest that the brain uses both control signal interactions and sensorimotor strategies to control and plan reach-and-grasp movements

DEDICATIONS

This work is dedicated to the memory of Eysha Bashiba. Thirty-five years ago, Eysha fought to defend her daughters' right to education. She stood bravely to face down poverty, illiteracy, traditional norms, and gender inequity. Her words still ring in my ears: "The strongest weapon a woman can have is education… we must apply the best of ourselves whether we succeed or fail."

I hold a special feeling of gratitude for my adored sister, Fatima AlOmawi, who had the arduous task of raising the family after the untimely death of our beloved mother.

I have no doubt that without these two great women, I could not have reached this point in my life.

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GLOSSARY OF ABBREVIATIONS

2D	Two dimensional movement
3D	Three dimensional movement
PPC	Posterior parietal cortex
SPL	Superior parietal lobule
SPOC	Superior parietal occipital cortex
PRR	Parietal reach region
V6A	Visual area 6
MIP/mIPS	Medial Intraparietal Sulcus in monkeys and humans respectively
LIP	Lateral intraparietal sulcus
AIP/aIPS	Anterior Intraparietal Sulcus in monkeys and humans respectively
7a	Brodmann area 7
S1	Somatosensory area 1
area 5	Brodmann area 5
PMd	Dorsal premotor cortex
PMv	Ventral premotor cortex
F5 (PMVr)	Rostral ventral premotor cortex
M1	Primary motor cortex
LOC	Lateral occipital complex
fMRI	Functional magnetic resonance imaging
TMS	Transcranial magnetic stimulation

EMG	Electromyogram
HD	High definition
LED	Light-emitting diode
ISCAN®	Eye movement monitoring instrument
OPTOTRAK®	Movement tracking instrument
IREDs	Infrared-emitting diodes
F	Gaze Stimulus/Fixating point
T	Reach Stimulus/target
VFB	Visual feedback
Open-loop	No visual feedback is available
Closed-loop	Hand and target visual feedback are available from the beginning until the end of a trial.
SD	Standard deviation
SE	Standard of Errors
LSD	Least significant difference
Sys-	Systemic
Var-	Variable
GDC	Grasp distance from stimulus centre
GAO	Grasp angle from orthogonal

CHAPTER ONE

1. GENERAL INTRODUCTION

Eye-hand coordination is essential for everyday interactions with the environment. We reach for, grasp, and manipulate diverse targets of interest without the awareness of the complexity involved in coordinating eye and hand movement. Several sensorimotor systems including visual, vestibular, and somatosensory, as well as eye, head, arm, and hand control systems are engaged in the eye-hand system. In addition, higher cognitive processing such as memory, attention, and decision-making are also involved in sensorimotor transformations (e.g., Cohen and Andersen, 2002; Crawford, Medendorp, and Marotta, 2004). Despite the extensive research focusing on these areas, it is still unknown how the brain deals with the complexity of the sensorimotor control of the hand, and how and where neural signals are transformed from sensory inputs to motor outputs. Studying how the brain coordinates eye-hand functions is important in behavioral neurosciences because it can help reveal the neural mechanisms underlying the broader concept of stimulus-based movement.

In visual stimulus–based movement, vision provides crucial information about an object's intrinsic and extrinsic properties, the object-environment, and body-object relative spatial relations. For example, to reach-and-grasp an object such as a door knob, the brain has to locate the knob's position in space and relative to the body. Further, it has to recognize the knob's size, shape, and orientation. To plan reach-and-grasp movement toward a doorknob, intrinsic information about the body is also required. The brain uses extrinsic sensory signals from the visual space and intrinsic signals from the body to generate motor outputs. Motor outputs are neural commands that cause contractions in the muscles around the joints (producing torques/rotational forces), subsequently producing joint rotations that transport the hand to the knob's location (reach component) and adjust hand posture to match the knob's size, shape, and orientation (grasp components).

The general purpose of this study is to investigate how visual inputs influence final hand movement, in particular grasp parameters such as location, orientation, and aperture. The results of this study provide novel insight into different aspects of eye-hand coordination and the mechanisms underlying reach-and-grasp movement control.

1.1. The Kinematics of Reach-and-Grasp Movement

Although humans reach for, grasp, and interact with objects smoothly and effortlessly, the kinematics and kinetics control of hand movements are complicated; for example, multiple joint rotations allow the hand to take an infinite number of orientations and paths to move between two points. Also, a desired hand rotation can be generated by an infinite combination of different levels of agonist and antagonist muscle activation around the joints of the upper limb. Movement and forces add complexity to hand movement control because transformation and coordination between kinematics (movement) and kinetics (forces) are required.

Despite the redundancy and complexity that underlie hand movement, humans are stereotyped in the movements they make. The brain seems to have constraint rules in controlling hand movement. One of the dominant constraint models is the specification of the limb end-point trajectory in space by following an approximately straight spatial path (Morasso, 1981). This straight path is consistent with the idea that arm movement is planned in extrinsic coordinates (Hogan and Flash, 1987). Other models assume that the motor system plans movement in joint (intrinsic) coordinates in term of muscle activation and joint rotation (Desmurget, Jordan, Prablanc and Jeannerod, 1997; Soechting and Flanders, 1992). The general idea of both models is the constraint of redundancy and the production of a smooth and accurate movement. Thus, the sensorimotor control system plans actions by using optimization principles such as minimizing the number of joints involved in the movement, avoiding biomechanical discomfort, and preserving an optimal final posture (Desmurget et al., 1995).

Several studies have used velocity profiles of a movement to describe the reach-and-grasp components (Bennett and Castiello,1994; Jeannerod, 1999). The transport velocity curve starts to accelerate from the beginning of the movement until it reaches its peak at about 50% of the movement time, and then it decelerates until contact is made between an end effector and a target. The curve takes a relatively symmetrical bell-shape, in which the acceleration and deceleration phases are relatively equal. The relatively symmetrical profile provides optimal control by minimizing the jerk, that is, the rate of change of acceleration (Flash, 1987; Jeannerod, 1999).

The submovement description of hand prehension was first reported by Jeannerod (Jeannerod, 1981). He suggested that reaching and grasping movements are controlled by two parallel channels for reaching and grasping. The basis of his hypothesis is that the circuit involved in reaching is concerned mainly with target location in space. Thus, the reaching circuit involves mechanisms that compute distance and the direction of visual cues with respect to an egocentric frame of references. In addition, this channel is engaged in activating the proximal joints and muscles. On the other hand, the grasping channel is involved in making direct contact with an object to accomplish a specific task such as manipulating, identifying, or lifting an object. The grasping channel is more concerned with the intrinsic properties of an object such as its shape and size. Furthermore, the grasping circuit is involved in activating hand joints and muscles (Jeannerod, 1999).

Jeannerod (1981, 1984) described grip aperture during movement. At the beginning of the movement, the distance between the thumb and index finger is progressively opened until it reaches its maximum opening at 70% of the movement. Then the gap between the two digits gradually decreases until contact with the object is made. Jeannerod (1984) noted that during the deceleration phase, there were several corrective movements even when the hand was invisible. The initial phase of the movement is preprogramed, and it transfers the hand to the target position. The second phase begins after the maximum aperture and is influenced by sensory feedback correction. Maximum grip aperture has been found to be influenced by changing object size (e.g., Jeannerod, 1981) and object shape (e.g., Gentilucci et al., 1991). Although the size of the maximum grip aperture increased linearly as a function of object size, the time to maximum grip aperture was the same for different sized objects.

A distinction between the intrinsic and extrinsic features of an object was made when investigators found that changing the amplitude of movement influenced only the transport but not the grasping component. Thus, wrist peak velocity increased with movement amplitude. In contrast, changing the size of the object affected the peak aperture but not the velocity of the movement. Spatial properties such as direction, distance, and velocity depend on an object’s location in relation to the body. These studies suggest that the intrinsic features of an object are not important for the spatial egocentric properties.

Many studies have tested the independence of reaching and grasping circuits by using a task involving manipulating the intrinsic features of an object such as size (e.g., Castiello et al., 1993; Paulignan et al., 1991a) or manipulating an extrinsic property such as location (e.g., Gentilucci et al., 1992; Paulignan et al., 1991b). Previous studies assumed that when there is an effect on one of the components (i.e., reach vs. grasp) but not on the other, these components must be independent.

Nevertheless, the results of these studies have been controversial. Some concluded that hand orientation is planned and organized independently from arm transport (Lacquaniti and Soechting, 1982; Stelmach et al., 1994), whereas others found that arm kinematics was affected by an object's orientation (Desmurget et al., 1996; Desmurget et al., 1995) Some research found that grip aperture was affected by object orientation (Galea et al., 2001; Gentilucci et al., 1996), and other studies have suggested that hand orientation and arm transport are integrated (Desmurget et al., 1998; Desmurget et al., 1996; Gentilucci, et al., 1996; Marotta et al. 2003). These findings have contributed to a debate about whether orientation is part of reaching (Desmurget et al., 1998) or part of grasping (Jeannerod, 1981), or whether it is an independent component of prehension (Fan et al., 2006).

Marotta et al. (2003) examined the contribution of the arm and forearm to final grasp orientation. They found that hand orientation was implemented from the beginning and throughout the movement. More importantly, they found that proximal and distal joints contributed to final grasp orientation but only accounted for about one-half of the orientation required to achieve the final grasp angle. The rest of the required orientation could be achieved by the hand. Previous research has suggested that the three components of reach-and-grasp movement (transporting, orienting, and opening of the digits) share common visual information (Mamassian, 1997). In addition, both the arm (upper and lower parts) and the hand interact and coordinate with one another to form the final grasp (Marotta et al. 2003; Crawford, Medendorp, and Marotta, 2004).

Although studies have shown that hand preshaping depends on a task's purpose (e.g., Sartori et al., 2011), Arbib et al. (1985) examined subjects who reached to grasp different cups for the same purpose. They manipulated features such as the size of the cup and the width and size of their handles. They found that although the final purpose of the movement was the same, subjects chose to grasp the handle with different grasp types. This study suggested that subjects use visual cues about an object to select their grasp type.

1.2. Movement Inaccuracies and Variability

Random disturbances of signal "noise" within the system and the environment limit our ability to perceive accurately and to act accurately and precisely (Faisal, Selen, and Wolpert, 2008). Movement inaccuracies can arise from different sources such as during sensory processing, sensorimotor transformations, and motor processing of the neural outputs of the motor system. In fact, noises occur randomly in the cellular machinery that processes information in every level of the nervous system, and these noises can accumulate during the network's interactions and nonlinear computations (Fasial et al., 2008).

Sensory noise contributes to variability in estimating internal (body/segment positions) and external (stimulus position) states. Noise produces errors in the internal representations of sensory information. Neural noise limits the accuracy and precision of estimates, for example, about how near an estimate of target location or hand position is to the true value, and how accurate the estimate is when repeated. Furthermore, neural noise associated with sensory inputs may impact the accuracy and precision of motor outputs (variability in endpoints) (Gordon et al., 1994; Vindras and Viviani, 1998). In addition, neural noise may affect the prediction of future kinematic variability in reaching (Churchland et al., 2006). Inaccuracies in internal representations that are computed during the sensorimotor transformation produce errors in motor outputs.

The motor system also produces neural noises. Variability in movement can arise from noise in motor commands (van Beers et al., 2004). Large motor commands tend to increase the amount of noise, which limits the accuracy and precision of the movement (Jones et al., 2002; Slifkin and Newell, 1999). Variation in the excitation of motor neurons and the recruitment of additional motor units that are needed to produce forces (Schmidt, et al. 1979; Jones et al., 2002) and to move additional degrees of freedom can cause an increase in movement variability.

Errors in movement can be measured in different ways. By averaging the final motor outputs across trials within and between subjects, we can examine the constant error in the movement. We can also examine the variability of final hand outputs by averaging the standard deviations in and between subjects. We can infer the coordinate system used in the movement from the patterns of constant and variable errors across subjects.

1.3. The Role of Sensory Feedback in Monitoring and Controlling Hand Movement

The brain uses internal models to control and guide hand movement. Feedforward and feedback mechanisms are used to control a movement. Feedforward control generates motor commands without taking into account the consequences of the movement. The motor commands generated by this mechanism are based on a desired state of the limb. Feedforward control plans the movement before the initiation of the movement and can produce errors. In contrast, feedback control corrects movement errors after they arise. The movement is monitored during and until the action is completed.

In reaching, the brain uses feedforward control to generate the initial part of a movement. As the movement progresses, sensory feedback becomes available, and this sensory feedback contributes to monitoring and correcting the movement. The disadvantage of the feedback mechanism is that it slows down the movement. However, the motor system integrates both feedforward and feedback mechanisms and uses predictions (by using internal models) to estimate the current state of the hand. The motor system uses these models to compensate for sensorimotor delays and reduces uncertainty (due to noise) in the estimate of the hand state.

The nervous system contains internal representations of the geometric parameters of the arm (such as the length of the arm's segments) and body segments. The brain uses these mathematical relationships between the joint angles of the arm to estimate the location of the hand. Internal models represent the causal relationship between a movement and its consequences. A forward model can estimate future sensory inputs based on motor outputs. This model can anticipate how the limb state will change as the result of a motor command. The brain uses an efference copy of a motor command to estimate the predicted state of the limb. In contrast, the brain uses inverse models to compute motor outputs from sensory inputs to estimate the changes in joint rotation needed to get the hand from its current to the desired position. These models are used to compute and update hand positions throughout the movement, especially in the final stage of the movement (when the hand is approaching the target).

Then the brain predicts the sensory feedback and the potential errors that would occur for the predicted estimate of the limb. The errors between the prediction and actual sensory feedback are used to correct the estimate of current hand position. This correction mechanism determines the relative reliance on sensory feedback and the efference copy. Proprioceptive feedback is crucial to update both the inverse models used to control movement and the forward models used to estimate a body part position as a result of a set of motor commands (Harris and Wolpert, 1998; Flash and Hogan, 1985; Blakemore, Goodboy, and Wolpert, 1998; Blakemore, Frith, and Wolpert, 1999).

Open- and closed-loop are often used to describe how the sensorimotor loops are controlled during a movement. In an open-loop condition, the sensorimotor loop is not completed by visual feedback. Movement accuracy declines when visual feedback (VFB) about the target is limited to a briefly flashed stimulus. This decline in accuracy is attributed to memory decay. Studies have found that subjects who reached toward a target after a delay period made large errors that correlated positively with the length of the delay (Gourtzelidis, Smyrnis, Evdokimidis, and Balogh, 2001). In an open-loop task, when we cannot see the hand, the brain uses proprioceptive signals to control and update hand movement (Ariff et al., 2002; Mehta and Schaal, 2002).

In a closed-loop task, the loop of sensorimotor transformation is completed by multiple sensory feedback (vision and proprioceptive signals). VFB about a target and the hand is available; thus, the brain can estimate the initial hand position either from visual information alone or by optimizing visual and proprioception information (Buneo and Andersen, 2006; Crawford et al., 2004; Flanagan, Terao, and Johansson, 2008; Sober and Sabes, 2003, 2005). Hand visual information is important to plan, guide, and enhance the accuracy of movement (e.g,. Blohm and Crawford, 2007; Paillard, 1996; Saunders and Knill, 2004).

Evidence has shown that people reach more accurately when they can see their hand before and during the movement, in contrast to not seeing their hand (Desmurget et al., 1995; Rossetti et al., 1995). Subjects tended to make large errors when VFB from the hand was partially or completely excluded (Jeannerod, 1999). Seeing the static hand briefly prior to the movement improves accuracy (Desmurget, Rossetti, Prablanc, Stelmach, and Jeannerod, 1995; Rossetti et al., 1995). A recent study (Dessing, Byrne, Abadeh, and Crawford, 2012) found that hand VFB suppresses gaze dependent errors, suggesting that gaze dependent errors could also occur as a misestimate of the hand’s location relative to the target.

Visual feedback about the target’s properties enhances the accuracy of movement, as subjects reached accurately toward visible targets (Berkinblit, Fookson, Smetanin, Adamovich, and Poizner, 1995) and when they looked at targets flashed for longer periods (Lemay and Proteau, 2001). Viewing the target promotes optimal use of visual information, which improves the accuracy of movement even when the hand is not visible (Prablanc, Pélisson, and Goodale, 1986).

1.4. Coding and Updating Spatial Locations

The spatial coding of a target position begins in the retina. When light falls on the retina and stimulates the neurons’ activity field, the visual image of an object is projected on the retinal surface. Because the fovea has a higher spatial acuity than peripheral parts of the retina, visual space is not represented equally in the visual cortex. However, the retinal signals are sent with the same retinotopic map to the visual cortices. Later, the retinotopic visual information is projected to other regions in the brain including the parietal and temporal lobes.

Nevertheless, the neuronal activities in cortical areas provide a different representation than the retina as they are influenced by extraretinal signals such as eye, head, or hand position. For example, when a stimulus falls within the receptive field of a neuron, the neuron will fire at different rates for different eye positions (Batista et al., 1999; Snyder et al., 1997). These neurons have a similar change in the gain as a function of head position relative to body or as a function of head position relative to the world (Zipser and Andersen, 1988; Andersen et al., 1998).

The modulation effects of extraretinal signals of the eye and head position on retinotopic activity are known as a “gain field.” The pattern of neural population discharges showed a Gaussian function of stimulus location in the retinotopic frame of reference. The firing rates of the neuronal population changed linearly with eye position. However, the response function did not change the peak of the tuning curve when eye position changed. These results indicated that the interaction between the target representation in the retinal and eye position was a multiplicative interaction (Andersen et al., 1997; Zipser and Andersen, 1988; Andersen et al., 1998; Snyder et al., 1997).

Every time the eye moves in space, the position of an object changes relative to the gaze (fovea). The brain maintains a stable representation of an object position in space by updating or remapping the visual space every time the eyes move. The brain estimates the prospective position of an object relative to gaze by using a copy of efferent signals for the eye movement to subtract the new eye position from the current target displacement (forward model); for example, when the target is displayed 10° to the right of gaze, and the eye is about to move 15° to the right, the new position of the target will be 5° left of gaze (Duhamel et al., 1992).

Evidence has shown that subjects pointed and reached more accurately when their gaze was aimed directly at targets. However, the accuracy of movement declined when gaze shifted away from the target (e.g., Bock, 1986; Enright, 1995; Henriques et al., 1998). Gaze dependent errors are characterized by overshooting a target, often in a direction opposite to the gaze by an amount varying systemically with gaze direction and amplitude (Bock, 1986; Henriques et al., 1998). An explanation for the accurate movement toward foveating targets could be that the acuity of vision is higher on the fovea than in the retinal periphery (Westheimer, 1984), and the representation of the fovea is thicker than the representation of the periphery in the primary visual cortex.

Errors in pointing and reaching toward peripheral targets occurred as a result of overestimating target displacements relative to the fovea, or overestimating target distance relative to gaze position (Bock, 1986, 1993; Henriques et al., 1998). Systematic errors occurred for retinal displacements as small as 5° and increased as the distance between the target and gaze increased until reaching a saturation point of approximately 15° (Bock, 1986; Henriques et al., 1998). The magnification effect is used to describe the mismatch between the retinal distance of the target and its cortical interpretation. The retinotopic peripheral magnification affects are different from the retinal central magnification (large fovea representation seen earlier in the visual cortex).

Furthermore, Henriques et al. (1998) found that subjects made the same gaze-dependent errors even when they foveated the target before shifting their gaze away from the target. These findings suggested that reaching movement was based on memory, which remaps the retinotopic representation relative to gaze direction after eye movement. This study and others (e.g., Henriques 2000; Pouget, Ducom, Torri, and Bavelier, 2002; Khan, Pisella, Rossetti, Vighetto, and Crawford, 2005) suggest that the spatial memory of a target location is stored and updated in the eye-fixed coordinate.

Most previous research has tested the direct effects of gaze direction on pointing and reaching tasks. No studies have directly examined the effect of gaze on final grasp amplitude or orientation. A study done by Selen and Medendorp (2011) investigated gaze and target attributes in a reach-and-grasp task. They suggested that both reaching and grasping errors are coded in the eye-centred coordinate. Moreover, the target’s orientation, similar to the target’s location, is coded and updated in the gaze-centred coordinate. However, this study did not independently manipulate the orientation of the target. They used a task in which the angle of grasp was biomechanically dependent on the reach angle.

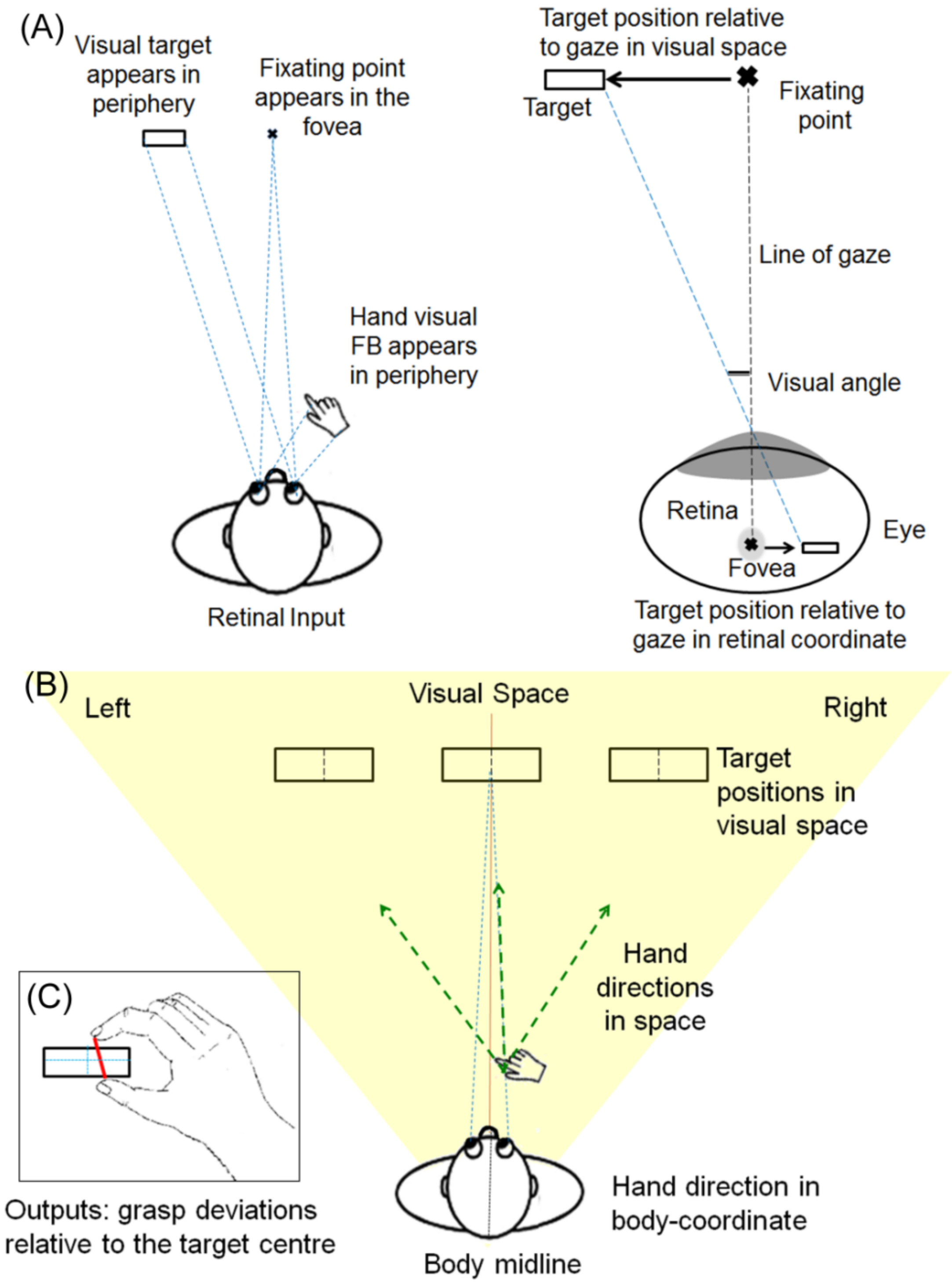

Figure 1 – Shows schematic illustrations of the definitions used in the experiment: the visual inputs, motor outputs, and their interactions. (A) shows a scheme where a subject is looking at a central fixation point and reaches for a left reach stimulus. The left

diagram displays the main visual inputs and their relation to the eye position. The right schematic shows the target position relative to the fixation point in space and in the retinal coordinate. Visual angle determines the distance between the target and the fixation point in space and in the retinal coordinate. Gaze direction represents the eye position in space and determines all other positions relative to the line of gaze. (B) shows the stimuli positions in visual space and relative to the subject's hand and body. (C) shows the grasp parameters at the end of "reach-to-grasp" virtual targets: subjects grasp the rectangle using the thumb and index finger. The red line connects the tip of the digits and defines the final grasp parameters: the size of the line is grasp amplitude, the midpoint of the line is grasp location, and the angle of the line is grasp orientation.

1.5. Sensorimotor Transformation of Visually Guided Movement

Sensorimotor transformation is the process of transforming sensory signals into a pattern of muscle activity. The neurological computations involved in integrating the sensory inputs of a target and the limb into a set of motor commands are not yet fully understood.

It is known that the desired grasp stimulus is localized in space relative to an egocentric frame of references; the target is localized relative to the eye, head, hand, and body (Figure 1). During this process, visual resources are combined. For example, the location of the target relative to the eye is computed from the location of the target on each retina together with the direction of gaze (see the right section of Figure 1A). The initial position of the hand can be estimated by combining visual inputs and proprioceptive signals and tactile sensations, each of which can provide information about hand position. Subsequently, the brain uses internal models to estimate the motor plan from the current positions of the target and the hand during the early stages of visuomotor transformation (Blohm and Crawford, 2007).

In the final stages of sensorimotor transformation, sensory inputs are converted into movement. The brain uses internal models to estimate the motor plan and to compute motor outputs that cover both the kinematic and kinetic aspects of movement (Kalaska, Scott, Cisek and Sergio, 1997; Shadmehr and Wise, 2005; Batista, Buneo, Snyder and Andersen, 1999).

Frames of reference are used to describe the location of an object with respect to a point within the body or in space. For example, one can describe the distance and direction of an object relative to the line of gaze, and the information about the object is coded in a gaze-fixed frame of reference. Any eye movement will affect the representation of that object in the gaze-fixed frame of reference. Consequently, the representation of the object is recalculated every time the eye moves (the explanation for this was previously mentioned in the text). Thus, frames of reference are used to describe the stages of sensorimotor transformation and to specify what is encoded in each area.

In the sensorimotor control system, there are multiple frames of reference within a coordinate system. For example, the position of a visual stimulus (a potential target for movement) is conveyed from visual inputs, while current information about hand position can be conveyed from two different frames of reference—from visual and proprioceptive inputs. Hand and target positions can be computed with respect to a number of frames of reference (Figure 1B). When a target and the hand are coded relative to a gaze fixating point, the spatial representations are coded in a gaze-centred representation. However, when target and hand positions are coded relative to a fixed point on the head, shoulder, or hand, the representations are coded in head-, shoulder-, or hand-centred coordinates, respectively. Any movement of these effectors (e.g., eye, head, shoulder, or hand) produces changes to the coordinate fixed to it (Buneo and Andersen, 2006).

Although all frames of reference could represent the same movement vector at a given time, the neural representation of that vector has different applications. For example, the motor vector can be represented as “retinal displacement,” i.e., target position in the gaze-centred frame of reference. Alternatively, the same vector could be represented relative to the hand, where the neural activity is fixed to the hand-centred coordinate (Buneo and Andersen, 2006).

A motor vector can be specified in terms of the difference in hand and target positions in the gaze-centred coordinate in the early stages of sensorimotor transformation (e.g., Buneo, Jarvis, Batista, and Andersen, 2002; Buneo and Andersen, 2006; Blohm and Crawford, 2007). However, to convey the extrinsic sensory inputs into muscle and joint movements, information about the relative positions of the eye, head, or hand are required. Consequently, at some points during sensorimotor transformation, the gaze-centred representation must be integrated with the proprioceptive signals. The integration of visual and proprioceptive inputs into joint-based coordinates could occur in the later stages of sensorimotor transformation (Beurze et al., 2006; Buneo and Andersen, 2006).

The distinction between the planning and execution of movement depends on the computation demands for a given task. These demands are solved by separate systems. During the planning stage, the computation of spatiotemporal description of a desired movement relies mostly on visual signals (Batista et al., 1999; Sober and Sabes, 2003; Shadmehr and Wise, 2005). However, in the movement stage, the motor vector is converted to motor commands that are concerned mostly with the details associated with movement implementation. During this stage, the extrinsic movement vector is transformed into an intrinsic, joint-based motor command (Kalaska, Sergio, and Cisek, 1998). These computations rely heavily on proprioceptive information (Sober and Sabes, 2003; Sainburg et al., 2003).

1.6. Cortical Areas Involved in Movement Control

Two streams are projected from the visual cortex: a dorsal visual stream to the posterior parietal cortex (vision for action) and a ventral stream to the infero-temporal cortex (vision-for-perception). The dorsal stream is involved in real-time control of actions, and its presentation of objects is continuously changed and updated. The dorsal stream transforms moment-to-moment information about an object to be used to guide immediate actions. In contrast, the ventral stream is concerned with presenting objects and in attaching meaning and significance to the objects across different viewing conditions over time. Thus, the ventral stream is involved in identifying and recognizing objects. The two streams are interconnected (Goodale, 2014; Goodale and Milner, 1992).

Although reaching for and grasping a doorknob appears to be a simple and direct action, the neural mechanism underlying the action is multifaceted, requiring the interaction of a number of different cortical areas. The dorsal stream in the posterior partial cortex (PPC) plays a crucial role in visually guided movement. Considerable evidence supports the notion of separate neural pathways for reaching and grasping. Reaching is computed by the medial parietofrontal networks including the superior parietal occipital cortex (SPOC in human brains/V6A in monkey brains) and its connections through the mid-posterior intraparietal cortex (the mIPS in humans/the MIP in monkeys) to the dorsal premotor cortex (PMd) (e.g., Vesia and Crawford, 2012; Crawford et al., 2011; Andersen and Buneo, 2002; Andersen and Cui, 2009; Batista et al., 1999; Kalaska et al., 1997).

In contrast, grasp movement originates from visuomotor control mechanisms and is computed by a cortical network in the lateral parietofrontal circuit including the anterior intraparietal sulcus (aIPS in humans/AIP in monkeys) and its connections to the ventral premotor cortex (PMv) (e.g., Murata, Gallese, Luppino, Kaseda, and Sakata, 2000; Culham, Danckert, DeSouza, Gati, Menon, and Goodale, 2003).

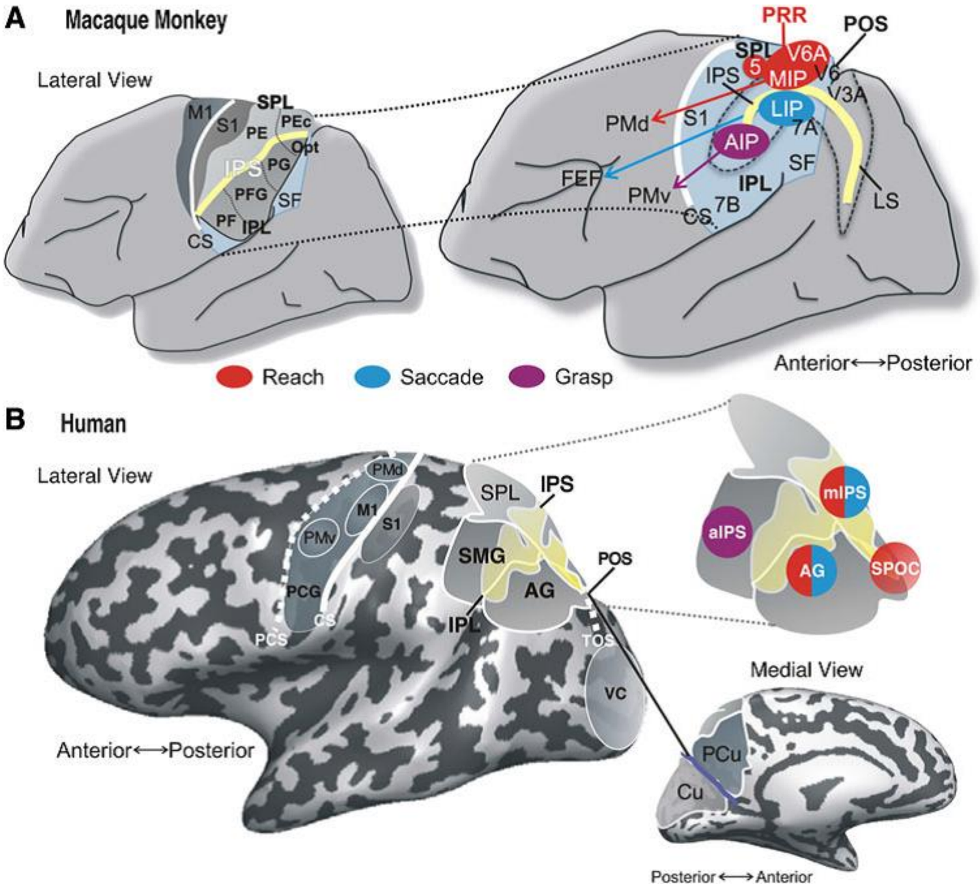

Figure 2 – Illustrations of a macaque monkey brain (A) and a human brain (B) show the basic anatomy of the visuomotor function in the posterior parietal cortex for saccade, reach, and grasp. In the right figures, the intraparietal sulcus (IPS) and the lunate sulcus (LS) have been opened to reveal the fundus and banks of each sulcus. CS=central sulcus; SF=sylvian fissure; POS=parieto-occipital sulcus; TOS=transverse occipital sulcus; PCS=postcentral sulcus; SPL=superior parietal lobule (PE, PEc); IPL= inferior parietal lobule (Opt, PG, PFG, PF); S= primary somatosensory cortex; M1= primary motor cortex; Brodmann areas 5, 7A, and 7B; V3A and V6A= visual areas; AIP =anterior; MIP= medial; LIP =lateral sections of IPS; VC= visual cortex; AG= angular gyrus; aIPS= anterior part of IPS; mIPS= midposterior part of IPS; SPOC = superior parieto-occipital cortex; PMd= dorsal premotor cortex; PMv =ventral dorsal premotor cortex; FEF= frontal eye fields; SMG =supramarginal gyrus; PCG= postcentral gyrus; PCu = precuneus; Cu= cuneus (the figure and captions are from Vesia and Crawford, 2012).

Figure 2 below shows the cortical areas involved in reach-and-grasp movement. The PPC and frontal premotor and motor areas contain neurons that strongly discharge during the planning and execution of a movement. The activities of neurons in the PPC and premotor areas convey information about the location of a target, the direction of the hand, and the configuration of the hand required to reach-to-grasp an object.

1.7. The Posterior Partial Cortex

The posterior PPC is involved in representing, storing, and updating spatial information about objects in the surrounding space. The PPC receives multisensory signals from different modalities such as vision, audition, and somatosensation. The PPC sends outputs to motor areas that produce movement plans (Batista et al., 1999; Buneo et al., 2002). Regions within the PPC such as area 5, the intraparietal sulcus, and area 7 are involved in encoding and planning movements of the eye and hand. Neurons in the lateral intraparietal bank of the intraparietal sulcus (LIP) discharge in response to visual (and auditory) and remembered targets (Colby and Duhamel, 1991). The LIP responds to a stimulus at a preferred retinotopic location (receptive field) (Goldberg et al., 1990; Colby and Duhamel, 1996; Mazzoni et al., 1996; Colby and Goldberg, 1999).

Andersen and Mountcastle (1983) showed that neurons in the inferior parietal lobule (area 7a) and the LIP received inputs about eye position and visual signals. The receptive field of these neurons changed as eye position changed (Anderson et al., 1985). Neurons in the LIP and area 7a encode representation of a stimulus location by combining signals about the stimulus position on the retina with eye position signals in the head-centred frame of reference (Andersen and Mountcastle, 1983; Andersen et al., 1990). Brotchie et al. (1995) found similar effects with changes in head orientation. The gain field modulated the target position in retinal signals, eye position signals, and head position signals in a body-centred coordinate. Eye and head position effects were the same for individual neurons regardless of whether the eyes or the head were used to direct gaze.

MIP neurons respond to objects in the visual field that are within reaching distance. The MIP codes object locations for reach actions. Thus, it is important for encoding arm movements (Snyder et al. 1997, Colby and Duhamel, 1991). MIP (as a part of partial reach region PRR) neurons tuned their firing rate as a function of the location of the reach stimulus relative to gaze, suggesting that reach plans in the PRR are encoded and kept in the eye-fixed frame (Batista et al., 1999). The advantage of keeping information about a remembered target (for reach) in an eye-centred frame is to update this information with incoming visual inputs every time the eyes move.

The parietal-occipital cortex (PO) receives visual inputs from the visual cortex mapped retinotopically (Galletti et al., 1999); however, the PO retinotopic map over-represents the visual periphery (Colby et al., 1988). Battaglia-Mayer et al. (2000) recorded the PO while monkeys performed delayed reaches to foveated and peripheral targets in light or dark conditions. They found that neurons in the PO were involved in early planning for arm movements. Neuron activity in viewing and reaching targets was similar for both reaches (in light and darkness). They also found that many neurons in the PO fired in a gain-like manner. The activity field of a neuron for a visual stimulus varied in magnitude as a function of eye position.

Fattori et al. (2001) found that V6A neurons were sensitive to the retinal representation of a target (Marzocchi et al., 2008) and modulated by eye position (e.g., Galletti et al., 1993). V6A neurons maintained their activity even after the target had disappeared (Bosco et al., 2014). Furthermore, V6A neurons were modulated by the relative position of the target with respect to the fixation point with mixed eye-centred and head-centred frames of reference (Marzocchi et al., 2008; Bosco et al., 2014).

Recently, V6A has been found to be involved in grasping and wrist orientation movement. Fattori et al. (2009) found that V6A neurons were influenced by hand orientation. These findings have been supported by other studies that showed induced lesions within the V6A produced deficits in reaching and grasping. Animals exaggerated finger extension and increased wrist orientation before making contact with an object (Battaglini et al., 2002). This evidence supports the involvement of V6A in both reaching and grasping movements. In fact, the interaction between the two circuits is necessary, and the V6A may play a cross-talking role in that it is crucial for coordination between reaching and grasping movements. The V6A may allow a functional coupling between the reaching, orienting, and grasping components of prehension. The V6A also could be involved in feedback monitoring and correcting of hand location and orientation (Fattori et al., 2009).

The AIP is involved in the early stage of the transformation from object representation to movement (Fagg and Arbib, 1998; Taira et al., 1990). The AIP was activated by the visual representation of an object when the hand interacted with an object and by the sight of an object even without executing a grasp action (Rizzolatti and Matelli, 2003). The activity of the AIP was related to distal hand and finger movements (Sakata et al., 1995; Murata et al., 2000; Taira et al., 1990). Studies have reported that neurons within the AIP were not affected by changing the position of an object in space.

Gallese et al. (1994) found that hand preshaping was impaired after muscimol injection in the AIP area in monkeys. The deficit was described as a mismatch between the intrinsic properties of the object (size and shape), or the animal was unable to reshape the hand to grasp the object; the animals either produced awkward grasping or failed to grasp the object. Furthermore, they found that precision grip was the most impaired grasp type.

Evidence for eye-centred representation of targets has been found in humans by using fMRI techniques. Merriam et al. (2003) studied activation in the PPC when subjects moved their eyes to either side of a remembered target. They found that the memory trace for a target was remapped in the contralateral side of the brain opposite to gaze direction. They found that the activity seen in the right LIP (when the target was visible and gaze was leftward of a target) disappeared when subjects gazed to the right of a remembered target location. However, the activity on the left LIP increased when the gaze shifted toward the right of the remembered target (ruling out the possibility of activation in the hemisphere due to a visual response). A follow-up study by Merriam et al. (2007) found similar fMRI activations in remapping targets as a function of gaze in extrastriate areas (V3 and V4) and in striate areas (VI and V2).

Medendorp et al. (2003) studied remapping in the PPC when subjects saccaded or pointed to remembered targets. For the saccade task, when subjects made an intervening eye movement to the opposite side of a remembered target, the activity of saccade-related areas of the PPC shifted across the hemispheres. For example, when the eyes moved across the target site after it disappeared, activity prior to the final saccade to the target shifted to the opposite side of the PPC. The same was found for arm-related areas in the PPC for pointing to the remembered target. Activity shifted across the hemisphere if the intervening saccades moved to the opposite side but not when the gaze remained on the same side. Again, this suggested that these areas in the PPC code and update the location of a remembered target relative to the final gaze. This study, consistent with neurophysiological studies, suggests that certain areas in the PPC code spatial memory in eye-centred coordinates.

Studies in humans have found that applying transcranial magnetic stimulation (TMS) to the mIPS and SPOC produced reaching errors. Vesia et al. (2010) used TMS to disrupt the mIPS and SPOC areas in a task that involved reaching toward remembered targets. They found that stimulating the mIPS increased the end-point variability for reaches and decreased the accuracy of reaches for contralateral targets. In contrast, stimulating the SPOC produced a deviation in the endpoint of reaches. Several studies have found that the SPOC is involved in encoding contralateral pointing and reaching towards peripheral locations (e.g., Culham et al., 2008; Fernandez- Ruiz et al., 2007; Filimon et al., 2009; Vesia and Crawford, 2012).

Khan et al. (2005b) tested optic ataxic patients with a damaged right PPC. Patients pointed to remembered targets that they viewed in one visual field, but then subjects pointed to the targets after they shifted their gaze to the other field (so the target fell in the opposite visual field). Patients produced larger errors when viewing and pointing to a target in their left visual field (contralateral to the damage) than when they viewed and pointed to a target in their right visual field. However, when patients viewed the target in their right visual field (target represented in their intact hemisphere) and then moved their eyes to the left (so the site of gaze was on the damaged PPC), the errors were as large as those made when the target remained in their contralateral visual field during viewing and pointing.

Pointing errors occurred because the remembered target for reaching was remapped in the damaged hemisphere. Conversely, when patients saw the target in the left visual field but before pointing they moved their gaze to the right (the site of gaze represented on the intact PPC), the errors were as small as when they viewed and pointed to the targets seen in their intact field (Khan et al., 2005b). These findings indicated that pointing responses were based on the remapped representation of the target relative to current gaze. The PPC has an important role in generating movement plans toward remapped target locations.

Follow-up studies found that patients with lesions in the superior PPC failed to reach accurately for objects that appeared in their peripheral vision. Reaching errors may result from impairments in spatial integration of both visual and proprioceptive information (Khan et al., 2007). Although these errors showed signs of multiple frames of reference, they depended on remapping target locations in the gaze-centred frame of reference (Khan et al., 2005a, b, 2007).

In humans, two fMRI studies examined aIPS responses to grasp type. In the first study, subjects were asked to reach and grasp objects of different sizes without receiving any instructions about the type of grasp or how to grasp the objects (Begliomini et al., 2007b). They found that subjects naturally chose precision grip for small objects and power grasp for large objects. In their second study (Begliomini et al., 2007a), subjects were asked to use precision grip for the large objects and power grip for the small objects. They found that, although the aIPS was tuned by both grip sizes, it was significantly more activated for precision grip than for power grip in both studies. These studies suggested that activation in the aIPS was independent of target size.

A recent study (Monaco et al., 2013) found that the SPOC and LOC (the lateral occipital complex in the ventral stream) processed common characteristics of objects for both grasping and viewing tasks. Their finding suggested that the effects on the SPOC are not only involved in sensorimotor feedback. The processing of the grasp-relevant dimension for viewing for potential action was evoked by object demands, even when the action was not explicitly planned. Monaco et al. (2013) showed that the LOC in the ventral stream is involved in coding mechanisms for reaching and grasping. Furthermore, the PPC and occipital temporal cortex might work in concert to extract grasp-relevant dimensions from overall object properties for potential actions.

Recent studies reported that the parietofrontal circuits for reaching and grasping were both activated in reach-to-grasp tasks. The relative activation was related to the degree of online control required by the movement (Grol et al., 2007; Verhagen et al., 2008). The PPC may be involved in online visual feedback (VFB) control of an ongoing movement (Vesia and Crawford, 2012). The PPC may use a feedforward strategy to predict the movement plan before the onset of movement (Wolpert, 1997; Desmurget and Grafton, 2000). The PPC also integrates visual and proprioceptive feedback signals, efference copies of ongoing motor commands, and internal models of limb dynamics.

The PPC uses these integrated signals to control ongoing movement (Desmurget and Grafton, 2000; Wolpert and Ghahramani, 2000; Blohm and Crawford, 2007). Lesion studies are consistent with these findings. These studies found that both brief lesions (by using TMS) and enduring lesions (pathological) in the PPC regions caused a disruption of online control of reaching (Wolpert et al., 1998; Desmurget et al., 1999; Pisella et al., 2000). Furthermore, neuroimaging studies have found that the SPOC was more active for reaching in the light (visual) than reaching in the dark (non-visual), whereas the mIPS is involved in both visual and non-visual reaches (Vesia and Crawford, 2012; Filimon et al., 2009).

Area 5 may be involved in the forward kinematics of the arm as it receives efference copy, visual, and proprioceptive inputs. The activity of area 5 neurons has been shown to be the best fit for forward movement control (Archambault et al., 2009; Mulliken et al., 2008). Several studies have reported that both the parietal lobe and the cerebellum are involved in forward models (Bastian, 2006) by monitoring and updating the internal status of the limb (Blakemore and Sirigu, 2003). Parts of the PPC have been found to be connected with the cerebellum. A recent study found connections between the LIP, MIP, and the cerebellum (Prevosto et al., 2010). The parietal lobe and the cerebellum form functional loops that are used to make online predictions of the sensory consequences of an action and to update a movement plan (Blakemore and Sirigu, 2003; Prevostoet al., 2010).

1.8. The Frontal Premotor and Motor Cortex

The premotor (PM) and the primary motor (Ml) cortices receive multisensory information and play major roles in movement preparation and execution (Sergio et al., 2005; Crammond and Kalaska, 2000; Weinrich et al., 1984). Arm motor-related areas in the PM and M1 are involved in planning both high-level kinematic parameters such as movement direction, amplitude, and speed (Kurata and Wise, 1988; Shen and Alexander, 1997; Moran and Schwartz, 1999; Crammond and Kalaska, 2000; Messier and Kalaska,

2000) and dynamic (kinetic) parameters (Sergio and Kalaska, 1997, 1998, 2003; Sergio et al., 2005).

The PM is involved in planning goal directed arm movements (Battaglia-Mayer et al., 2000; Graziano, 2006; Pesaran et al., 2006), and it is divided into sub regions including the ventral premotor cortex (PMv) and the dorsal premotor cortex (PMd). The activity of the PMd is correlated with the direction and amplitude of proximal joints during reaching movements (Caminiti et al., 1991; Kalaska et al., 1997; Wise et al., 1997). Neurons within the PMd (F5) were activated by distal joint movements. Interestingly, these neurons were not activated by individual finger movements, but they were activated by the grasping action as a whole (Raos et al., 2004).

Weinrich and Wise (1982) recorded the activity of cells in the PMd and found that neurons were activated during preparation for movement. More than half of these neurons showed greater response to motor instruction cues (Boussaoud and Wise, 1993a; Hoshi and Tanji, 2006). PMd responses reflected the motor significance of instructional cues (Boussaoud et al., 1996). Activity in the 5d, PMd, and M1 was related to the kinematics planning of the intended movement (Crammond and Kalaska, 1989).

Wise and Mauritz (1985) tested whether the neuronal activity in the PMd was sustained when monkeys reached toward a remembered target location. Their hypothesis was that if neurons participate in movement planning, neural activity should not be affected by a target’s disappearance before the go signal. They found that PMd neurons were not influenced by the visibility of the target; instead, the PMd was modulated by movement direction. However, changing the location of the target caused significant changes in preferred direction. Thus, the preferred direction of PMd neurons was related to the motor vector of the intended reach. Moreover, the PMd coded movement position relative to the hand (instead of coding target location in the visual coordinate). Neurons were activated in relation to the direction and magnitude of the limb movement (Boussaoud and Wise, 1993a, b; Caminiti et al., 1991; Crammond and Kalaska, 1994; Kalaska et al., 1997).

A recent study (Pesaran, Nelson and Andersen, 2006) tested whether the PMd used a similar eye-fixed reference frame to code the target as is used by the PPC. They reported that PMd neuronal activity was modulated as a function of both gaze and hand position relative to the target. Thus, the PMd encodes the relative positions of the target, the hand, and the eye. Therefore, the activity of PMd neurons did not code the target location in a single reference frame; instead, it represented all the variables (target, hand, and eye position) that are crucial for hand movement. The PMd is involved in representing the target with respect to gaze and hand position. In addition, the PMd contributes in planning hand movement (Riehle and Requin, 1989; Hoshi and Tanji, 2000).

Neurons in the PMd are involved in suppressing any prepared but unused movement plans (Koch et al., 2006). The PMd is also involved in the process of selecting an appropriate action from multiple options. Cisek and Kalaska (2005) found that multiple reach options were initially specified in the PMd and then gradually eliminated. The neurons initially represented potential reach directions, and then represented the direction of a selected target.

Scott, Sergio and Kalaska (1997) tested the correlation of the sensitivity of neural activity in the PMd, M1, and area 5 to extrinsic versus intrinsic frames of references by training monkeys to reach using similar hand trajectories but different arm orientations. They found that activity in the PMd, M1, and area 5 was modulated by arm orientation. While the magnitude of the activation was less in the PMd than in the MI (Scott and Kalaska, 1997), neurons within the PMd showed activity that closely resembled the activity in the M1. The activity of PMd and M1 neurons was heavily influenced by preferred direction (Caminiti et al., 1991), arm posture, and hand trajectory (Scott et al., 1997).

The PMv also has been found to be involved in preparing arm movements. Kakei et al. (2001) studied neuronal activity during wrist movements with different arm postures. They found that the majority of PMv neurons were selective for the direction of the hand. Neuron modulation was independent of posture. These findings suggest that the neurons encoded wrist movement in the extrinsic frame of reference. Subsequent studies extended this study by examining whole-arm movements. They found that PMv neurons were involved in trajectory formation in space (Schwartz et al., 2004) and in the direction of visual information about hand motion (Ochiai et al., 2005). PMv neurons were not affected by changing gaze direction. PMv neurons were able to encode the spatial locations of a visual stimulus in near space even when the retina inputs constantly changed as a result of eye movement (Graziano and Gross, 1998).

Kurata and Hoshi (2002) recorded neurons in the PMv in monkeys trained to reach a target with prism goggles. The prism was used to dissociate motor space from visual space. They found three classes of neurons in the PMv. The neurons represented the target location in visual space, in motor space, and in both. The PMv was involved in transforming information about the target in space into motor signals required for movement. Thus, the PMv matched visual space to motor space. Boussaoud and Wise (1993a, b) found that the majority of PMd neurons represented the motor significance of visual signals, whereas PMv cells reflected the visuospatial information of visual cues such as the processing of the dimensional features of a target, wrist orientation, and finger configurations (Raos et al., 2006). Moreover, inducing lesions in the PMv (F5) area produced grasping deficits similar to the deficits associated with the AIP lesions (Fogassi et al., 2001).

The M1 has been found to be involved in generating muscle contractions and in contributing to higher levels of control such as planning, organizing, and coordinating actions. Neural activity of M1 neurons was correlated to the extrinsic spatial kinematics of hand motion such as movement direction and distance, target location, speed, and velocity (Moran and Schwartz 1999; Ashe and Georgopoulos 1994).

Detailed representation of the moment-to-moment spatiotemporal trajectory of hand movement suggested that the M1 contributes to the early stage of visuomotor transformation. Neurons in the M1 encode the direction of movement by a vectorial code. Different neurons have different preferred directions in space, which are distributed uniformly in space. Georgopoulos et al. (1989) found that population vectors (the sum of all the single neuron vectors) accurately predict the direction of hand movements in Cartesian coordinates.

Moreover, studies that distinguish between extrinsic and intrinsic movement parameters have found that the M1 also encodes hand movement in shoulder-centred and muscle-based (intrinsic) coordinate systems. Caminiti et al. (1990, 1991) extended the study done by Georgopoulos et al. (1988) by training monkeys to reach in the same direction but toward three different locations in a 3D workplace. Their assumption was that if M1 neurons encode hand movement in a Cartesian coordinate, neural activities must be the same for all different locations. The results showed that the preferred direction and amplitude of M1 neurons were directionally tuned in some locations in space but not in others. The preferred direction of population neurons rotated from one cube to the next along the vertical axis, which corresponded to the shoulder joint movement. Caminiti et al. (1990, 1991) concluded that single M1 neurons also encoded the vectors of whole arm movement in the shoulder-centred coordinate.

Scott and Kalaska (1997) recorded the neural activities of M1 neurons while monkeys reached in eight different directions using the same 2D hand paths but with the arm in two different postures. They assumed that if M1 neurons encoded motor output in the hand-centred coordinate, neural activity must be influenced by arm posture. Scott and Kalaska found that changing arm posture caused changes in the activity of single M1 neurons. The changes in neural activity correlated with posture-dependent changes in the intrinsic coordinate as the hand moved along the same spatial path.

However, Scott and Kalaska’s (1997) study could not exclude the correlation of neural activities with the hand-centred or shoulder-centred coordinate system. They found that when the arm was in the parasagittal posture, changes in arm posture also altered the overall distribution of preferred directions as previously found in Georgopoulos et al. (1982, 1988). However, when the arm was in the horizontal plane, the change in preferred direction distributions reflected the reduction of M1 neural activity associated with the degree of shoulder rotation.

Wu and Hatsopoulos (2006) found that the preferred direction of a few M1 neurons remained constant in all sectors of the grid in the hand-centred coordinate. Also, the tuning curves of other neurons rotated in the horizontal plane when the hand was in different parts of the grid. In some neurons, modulation was correlated with the shoulder-centred coordinate. The results suggested that neural activity was influenced by arm posture in the intrinsic-based coordinate. Neural activity in M1 neurons did not exclusively represent hand movement in either extrinsic or intrinsic coordinates.

Sergio and Kalaska (1997) recorded the activity of M1 neurons in a task in which monkeys were trained to use the whole arm to generate static forces at the hand in constant spatial directions while the hand was in one of nine different spatial locations. They found that both the firing rate of M1 neurons and EMG muscle activity were modulated by both hand location and by the direction of static force. Sergio and Kalaska found that the M1 is involved in transforming neural signals from an extrinsic-to-intrinsic coordinate.

The MI could contribute to an internal model of limb mechanical properties that is necessary to resolve sensorimotor transformation and to compensate for the mechanical properties of the limb. Moreover, M1 intrinsic representation incorporated information about limb biomechanics either provided by proprioceptive feedback or acquired by adaptive learning mechanisms (Sergio and Kalaska, 1997).

Sergio and Kalaska (2003) and Sergio et al. (2005) studied M1 activity in monkeys performing similar reaches and producing isometric forces. Sergio et al. examined monkeys exerting isometric output forces at the hand in eight directions in a horizontal plane against a force that was positioned in different locations. These isometric-force tasks avoided the confounding effects introduced by the dynamics of whole-arm movements. They found that the directional tuning and amplitudes of single cells changed in a complex pattern. However, M1 neurons were influenced by posture, isometric force, and movement task. Cell directional tuning tended to shift systematically with hand location. Directional modulation was less pronounced before force onset than after force onset. The muscles of the arm showed similar effects, suggesting that hand biomechanical factors altered the task-related activity.

The results suggested that the initial kinetics of reaching movements did not fully account for dynamics-related activity prior to the initial motor output. The M1 incorporated dynamics-related activity in real time during motor behavior. The M1 integrated information about arm geometry, the mechanical properties of the arm, and the causal forces necessary to produce the desired motor output. These results provided further evidence that the MI contributes to the transformation from extrinsic to intrinsic representations (Sergio and Kalaska 1997, 2003; Sergio et al., 2005).

1.9. The Effect of Target Location on Reach-and-Grasp Movement

Studies have found that reaching and pointing errors associated with target location changes were confounded with errors related to different gaze directions. These studies avoided the interaction of target and gaze on endpoint errors by fixing target location in the centre of visual space or in relation to the body. However, target location has been found to modulate the accuracy of movement independent of gaze direction. Subjects tended to mislocate targets displayed farther away from the midline of the body. Subjects undershot the target with large arm displacement (Bock and Eckmiller, 1986; Prablanc et al., 1979a,b).

Paulignan et al. (1997) examined the effect of object location and size on final grip opposition axis (the line that connects the thumb and index finger). They found that reach and grasp components were influenced by object position. Movement time, time to peak velocity, and time to maximum grip aperture were also affected by the object's location independent of the object's size. The variability of wrist and fingers decreased before contact was made with the object. The orientation of the grip axis was found to change by about 10° from one object position to the next when an object-centred frame of reference was used. However, orientation remained relatively invariant for different object positions in a body-centred frame (with the head or the forearm as a reference).

1.10. Specific Introduction

In order to pick up or manipulate a seen object, one must use visual signals to aim and transport the hand to the object's location (reach), and configure the digits to the shape of the object (grasp). Considerable evidence has suggested that there are separate pathways for reach and grasp. The medial parietofrontal pathway is involved in controlling reaches (e.g., Vesia and Crawford, 2012; Crawford et al., 2011; Andersen and Buneo, 2002; Andersen and Cui, 2009; Batista, Buneo, Snyder, and Andersen, 1999; Kalaska et al., 1997). Early portions of this pathway show eye-fixed sensory receptive fields and gaze position modulations suitable for aiming in visual space (Snyder, 2000; Batista et al., 1999; Buneo, 2002; Medendorp, Goltz, Vilis, and Crawford, 2003), whereas the later portions show stronger motor tuning and modest gaze modulation (Graziano and Gross, 1998; Cisek and Kalaska, 2002).

In contrast, the lateral parietofrontal circuit shows activity related to grasp and grasp-relevant visual parameters, including stimulus orientation (Muratta, Gallese, Luppino, Kaseda, and Sakata, 2000; Culham, Danckert, DeSouza, Gati, Menon, and Goodale, 2003; Monaco, Cheng, Medendorp, Crawford, Fiehler, and Henriques, 2013). To date, no studies have shown gaze-direction dependence in human AIP responses. In real world conditions, all of these signals (gaze, reach, grasp) must interact to provide accurate eye-hand coordination (Buneo and Andersen, 2006; Crawford, Medendorp, and Marotta, 2004). One possible site for this interaction is V6A, which has recently been shown to share reach, grasp, and gaze signals (Fattori, Breveglieri, Marzocchi, Filippini, Bosco, and Galletti, 2009). However, the behavioral influence of such interactions has not been comprehensively studied in humans.

In some reach behaviors, gaze remains locked on the target object for the duration of the task (Neggers and Bekkering, 2000), but often gaze deviates from the target by the time the reach begins (Flanagan and Johansson, 2003). Humans make errors in reach or pointing direction when they fixate gaze toward a central target and reach toward a remembered peripheral target (e.g., Bock, 1986; Enright, 1995; Henriques et al., 1998; Vesia et al., 2010). Since this could be related to either visual or motor factors, many studies have attempted to isolate the influence of gaze direction by asking healthy or brain-damaged subjects to reach or point toward a central target while varying gaze direction (e.g., Bock, 1986; Enright, 1995; Henriques et al., 1998; Henriques, 2000; Pouget, Ducom, Torri, and Bavelier, 2002; Khan, Pisella, Rossetti, Vighetto, and Crawford, 2005; MacQuire and Sabes, 2009).

These studies almost universally report a directional overshoot of remembered visual target direction relative to gaze direction. It has been argued that this represents an overestimate of target direction (Bock, 1986; Henriques et al., 1998) or an underestimate of gaze position (MacQuire and Sabes, 2009) in the transformation of target location into reach coordinates. However, recent data suggest this might be due to an error in the transformation of hand position signals into visual coordinates (Dessing et al., 2012). In pointing movements, this pattern of gaze-centred overshoot was independent of actual target location in space (Henriques et al., 1998), but this issue has not been investigated in a more complex reach-to-grasp behavior. In principle, one might expect the same pattern of gaze-centred overshoots, but this cannot be assumed since aiming a grasp toward a non-point stimulus adds more degrees of freedom and additional computational and biomechanical constraints.

Still less is known about the influence of gaze direction on grasp parameters. Selen and Medendorp (2011) found an influence of target direction relative to gaze on the horizontal angle of grasp but in their task, this co-varied biomechanically with the horizontal angle of reach errors. Paulignan et al. (1997) investigated the effect of target position and size attribute in final grip parameters and found that the position, size, and orientation of the grip was modulated by changing target position and size. However, they did not study the effects of manipulating target orientation on final grasp parameters.

To our knowledge, no study to date has directly examined the influence of gaze direction on a grasp parameter that is independent of reach, such as grasp orientation around the axis of the wrist or grip aperture (i.e., the distance between thumb and forefinger in precision grip). On computation grounds alone, such parameters might be computed independently from gaze direction and/or stimulus location (Marotta et al. 2004), but in a biological system that shares all of these signals and is known to make errors in location, this cannot be taken for granted.

The purpose of the current study was to investigate the interactions between object location, gaze direction, reach, and grasp parameters at the behavioral level, and use the data to interpret the level of interaction that occurs in the underlying control system. Specifically, we examined the influence of horizontal stimulus location and stimulus orientation on 1) grasp location, 2) grip amplitude, and 3) grasp orientation.

We used a semi-pantomime stimulus (subjects reach toward oriented stimuli on a computer screen) in order to eliminate any useable somatosensory feedback and avoid injury; we also used virtual targets to be able to compare our data with previous studies that tested the effects of gaze on final movement accuracy (as most of these studies used virtual targets). Finally, since it was difficult to predict exactly how subjects would behave in this paradigm, we investigated and compared two VFB conditions: open-loop (complete darkness after stimulus presentation) and closed-loop (presence of hand and target VFB) conditions.

Based on previous research, one can expect that the motor outputs for the reach component could take the same pattern of gaze-centred overshoots. However, asking participants to reach-and-grasp a rectangular stimulus might require a different sensorimotor control mechanism than a simple reaching or pointing task. Therefore, overshoot effects could not be assumed for a grasping behavior. Thus, we conducted exploratory research; we assumed there would be differences between the groups, but we could not make a presumption about the direction of the effects.

CHAPTER TWO

2. METHODS

2.1. Participants

Ten right-handed subjects participated in the experiment. No participants reported neurological or other relevant medical deficits, and all had normal or corrected-to-normal vision. Of the original number of subjects, nine were naïve, one subject was aware of the nature and design of the experiment and was excluded from the experiment after he reported making an effort to predict and control hand movement trajectories. This participant's performance also seemed to differ from the performance of the rest the subjects. We excluded two additional participants because they were not able to follow the instructions for performance. One of them consistently initiated hand movement before the go signal, and the other had inaccurate eye performance. Seven participants remained (three females and four males). Their ages ranged from 20 to 31. Informed consent was obtained from all participants after the instructions were given. The experimental procedures were approved by the York University Human Participants Review Subcommittee.

2.2. Experimental Setup

Except where indicated otherwise, all experiments took place in a completely dark room. Participants were seated in an upright position in front of a table supporting most of the apparatus used in the study (see Figure 3). The height of participants' chairs were adjusted so as to comfortably stabilize the chin in a custom-made head rest mounted on the table. The head rest was positioned to align the midpoint of the eyes ($41cm$) to the centre of a TV screen ($70cm\ x\ 40cm, Sony\ TV, HD\ 32'' - 1080\ p$). The screen was covered with a dark coating to eliminate extraneous stimulus glare and maintain darkness in the workspace. The initial hand position for each movement trial (as shown in the left panel of Figure 3) was indicated by a green LED light attached to a short vertical rod mounted halfway between the base of the head rest and the TV screen ($13cm$ from the screen). Two light bulbs were placed in the background and flashed between trials to prevent dark adaptation.

$2D$ eye motion was measured using the *ISCAN*® infrared eye tracking system, mounted on the table under the left corner of the screen. 3D hand motion was measured by an *OPTOTRAK* system (Northern Digital, Inc., Waterloo, ON, Canada; 3020 camera) mounted on an adjacent wall, with the participant and table oriented with respect to the cameras to minimize obstruction between the hand and *OPTOTRAK* sensors. To track digit $3D$ movement, two rigid bodies were constructed and attached to the distal part of the right thumb and index finger. A cluster of eight infrared-emitting diodes (*IREDs*) was glued to each digit's rigid body (Figure 3).

2.3. Visual Stimuli

Two visual stimuli were simultaneously displayed on the screen (Figure 4): a white dot for gaze fixation and a rectangle ($1.5cm \times 3.5cm$) with white borders functioning as a virtual reach/grasp target. In the open-loop condition, the stimulus rectangle was flashed briefly in the dark (see next section for details), whereas in the closed-loop trials, participants were able to see the targets and their hands before and throughout the movement. The rectangle remained visible, and the hand was illuminated using four white LED lights that were attached to the corners of the screen,

Figure 3 – Shows the experiment apparatus and the hand movements from initial (right panel) to final (left panel) hand positions. The actual experiment was held in complete darkness, and participants could see neither their hand nor any allocentric visual cues (unlike in the photographs).

and they were directed toward the initial hand position and movement path.
The sources of the lights were covered by cone-like black sheets. The lights were controlled by a computer. Both reach and gaze stimuli were displayed at one of three locations on the screen: either in the centre or at 20 visual degrees ($15cm$) left/right of the centre. The gaze or reach stimulus could appear at the same location together in any of these three locations or in any other combination of different locations. In addition, reach targets were displayed semi-randomly on one of three orientations (horizontal and at $45°$ clockwise and counter-clockwise).

These combinations of three target orientations, three target locations, and three gaze fixations were repeated nine times, resulting in a total of ($3 \times 3 \times 3 \times 9 = 243$) trials for each of the two VFB conditions, in which the order of conditions was randomized across subjects. Each session lasted about 145 minutes, including calibration procedures and rest periods, and was repeated on three days.

2.4. Experimental Paradigm

Participants were instructed to reach and "grasp" the surface of the TV screen at the remembered location and orientation of the rectangle at its narrow width with the right thumb and index finger (as shown on Figure 3). Participants were instructed to reach-and-grasp the target as accurately as possible, as if it were a real object, and with their natural speed while maintaining their gaze fixated on the fixation point.

Participants started the trial by placing the tips of their thumb and index finger on the initial position rod. The gaze fixation stimulus (F) was displayed on the screen for the entire duration of the trial. $500ms$ after the fixation stimulus appeared, the target (T) was displayed. After another $800ms$ ($\pm 200ms$ to avoid anticipation).

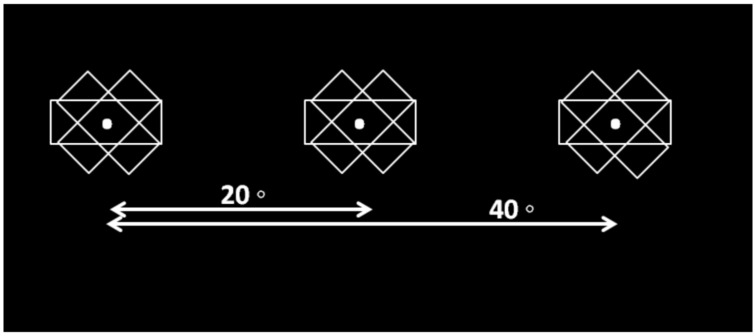

Figure 4 – Shows the possible stimuli locations for eye fixation and reach target shown on visual angle, and possible target orientations (horizontally and 45° clockwise and counter-clockwise). The white dot represents the fixation point, and the rectangular is the reach stimuli.

The participants heard a brief “beep” (see vertical dashed lines in Figure 5) that signaled participants to reach toward the target location and orientation. At the onset of the “beep,” the target visual condition was manipulated. Thus, the target disappeared (was turned off) in the open-loop condition or remained on in the closed-loop condition.

Participants were asked to keep their fingers touching the screen and maintain their gaze on the fixation target until they heard another sound signaling the end of the trial. After a second “beep” signaling the end of the trial, participants returned their hand to the home position and waited for the next trial. The closed-loop trials were identical to open-loop trials except (as described above) the stimulus rectangle and hand were visible for the entire duration of the trial. All participants were required to practice these paradigms for 15 minutes before the first recording session to avoid confusion during the experiment. Figure 5 below provides a schematic illustration of one combination used in the open-loop condition.

2.5. Data Collection and Analysis

Three computer stations were used to collect the data. Trial conditions and display orders were controlled by a custom-written C++ program. This program also sent synchronization pulse sampling at $1000Hz$ to $OPTOTRAK's$ digital acquisition unit to define trial event codes. The OPTOTRAK’s acquisition unit also received signals from the eye tracker program to define the horizontal and vertical position of the participants’ eyes. The $3D$ motion of the $IREDs$ was recorded at a rate of $100Hz$. Calibrations of the fingertip and eye recordings were completed before starting the actual recordings. The finger outline was defined as positions at $0.1mm$ intervals along a reconstructed $2D$ polynomial virtual point.

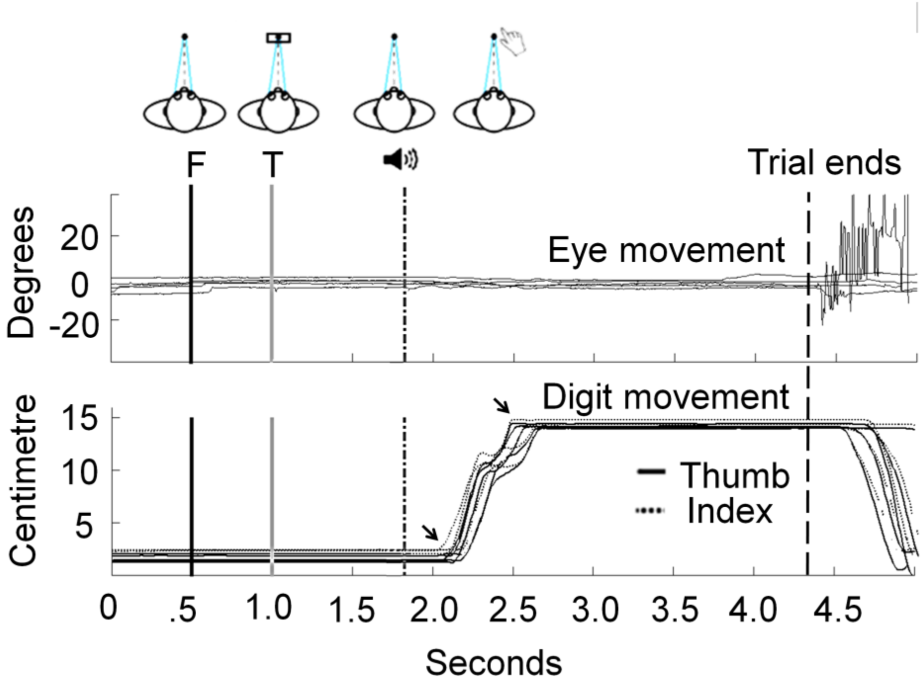

Figure 5 – The upper schematic shows one combination of the paradigm: the fixation stimulus (dot) displays for 500ms before the target appears. After 800±200ms, an auditory tone (🔉) was released, signaling the subject to reach and grasp the target. At this stage, the visual feedback conditions were manipulated. The upper schematic is for a subject gazing to the centre and reaching towards a remembered horizontal target positioned on the right. The two panels show five trials for the subject represented in the upper schematic. The upper panel shows the digit positions on the y-axis (upward) as a function of time. The arrows indicate the beginning and the end of the movement. The lower panel shows the horizontal eye positions measured in visual degrees as a function of time.

These points result in the best fit of an eight order of the rigid body coordinates of the finger markers (Dessing et al. 2012). For eye calibration, five vertical and horizontal fixation dots on the screen were used.

Because participants' heads were fixed in space, gaze direction was equal to eye position in space. The midpoint of the eyes was adjusted to the centre of the screen, and the initial hand position was adjusted to the body midline (as illustrated in Figure 2). Kinematics data were represented in a Cartesian coordinate frame. The upper left corner of the screen was considered as the origin of the spatial coordinate with the positive x-axis pointing rightward, the positive y-axis pointing downward, and the positive z-axis pointing to the screen. However, for simplicity and graphing purposes, this coordinate system was then shifted to originate at the centre of the screen. The negative direction of the horizontal axis points to the left, while the positive direction points to the right. The negative direction of the vertical axis with data points downward, and the positive data points upward.

The eye and digit kinematics data were analyzed offline by a custom-written program in *MATLAB*. Final reach positions were defined as the contact position of the digit tips on the screen. This was determined off-line as the point in time when digit movement reached a stable position along the z-axis (forward axis toward the screen). Since we only manipulated gaze and target positions along the horizontal dimension, likewise, only horizontal grasp locations were analyzed. Final grasp location, grip amplitude, and orientation were parameterized as the mid-point, length, and angle (respectively) of the line connecting the thumb and index finger (see Figures 7 and 8 for examples).

The motor outputs were qualified as the grasp parameters relative to reach stimulus properties (the centre of the target as well as the width and orientation of the target). The grasp location deviations from reach stimulus properties were qualified with respect to the gaze and hand directions. For example, undershooting the target centre was qualified when the deviation shifted toward the gaze or hand, whereas overshooting the target centre was identified when the deviation shifted away from the gaze or hand positions.

We did not subtract closed-loop performance from open-loop performance to obtain grasp "errors" because 1) we did not wish to assume that closed-loop trials were free from error in this task; 2) we wished to consider visual feedback as an experimental manipulation; and 3) there are a variety of ways to pick up an object, so one cannot assume that small deviations in performance are errors. Therefore, we instead calculated behavioral "deviations" relative to theoretical ideals.

Grasp location deviation was calculated on the horizontal axis relative to the reach stimulus centre as "grasp distance from stimulus centre" (GDC). It was calculated by subtracting the midpoint of grip location from the target centre position. Grasp angle deviation was qualified relative to the orthogonal angle of reach stimulus orientation as "grasp angle from orthogonal" (GAO). It was computed by subtracting grasp orientation from an ideal grasp orientation orthogonal to the target orientation (i.e., GAO = observed grasp angle $-$ target orientation $+$ 90°).

It was not possible to establish "ideal" grip amplitude, since subjects never actually gripped a physical stimulus, but as a baseline one may note that the stimulus width ($1.5cm$) plus the typical distance between digit *IREDs* and thumb/finger surfaces was approximately $2.5cm$. Therefore, for grasp parameters, we only compared values between different experimental conditions. These parameters were calculated and averaged separately for open-loop and closed-loop trials for the purpose of statistical comparison within and across conditions.

Both the accuracy (systemic) and the precision (variable) of grasp components were analyzed. Both are the average of the means across subjects (across trials and within subjects). The systemic (Sys-) data was calculated by first computing the mean across trials for individual subject and then calculating the average of the means across subjects. The variable (Var-) data was calculated by averaging standard deviations (SD) across trials for individual subjects and then computing the average of SD means across subjects.

Only trials in which movement started after $100ms$ from the "Go" signal were included in the analysis (to ensure that participants did not start moving while the target was still visible). Trials were also excluded whenever participants failed to maintain gaze on the fixation dot at any time from the start of the trial up until the point of contact/data analysis of the fingers with the screen. Finally, trials were excluded whenever there was noise or unclear eye recording signals, or when there were missing traces of 3D finger motion at the beginning or the end of the reach movement.

SPSS software was used for statistical analysis. A full factorial linear mixed model analysis was used with four fixed independent factors: target orientation, target location, and gaze direction, with "participant" considered to be a random factor. Least significant difference (LSD) was used to adjust for multiple comparisons. The alpha significant level is at 0.05 (our statistical data analysis method is consistent with the method used by Dessing et al. (2012).

CHAPTER THREE

3. RESULTS

3.1. Overview of Reach Trajectories

Before focusing on the main aims of this study (grasp reach parameters at the reach endpoint), we considered some example trajectories that helped to illustrate the general reach behavior of our participants in this task. Figure 6 (A, B) shows the digit trajectories in three open-loop example trials, in which subjects reached toward the remembered location of a left, centre, and right target. In each case, the stimulus was oriented horizontally, and gaze was maintained at the centre of the stimulus. The short black lines connect the finger and thumb position spaced at 20ms temporal intervals, so the distance between the lines are proportionate to velocity. Panel A shows these from behind (vertical vs. horizontal), whereas panel B shows the side view (vertical vs. depth axis; here only the centre trajectory is shown because the others were very similar and overlapped).

All of our subjects reached and grasped the different target locations and orientations with index finger on top relative to the thumb. As one can see, the hand showed an initial rapid acceleration, showing a fairly constant vertical velocity through space (with a relatively slow adjustment in grip orientation) and then slowed near the top, as if the participant was placing it in front of the stimulus.

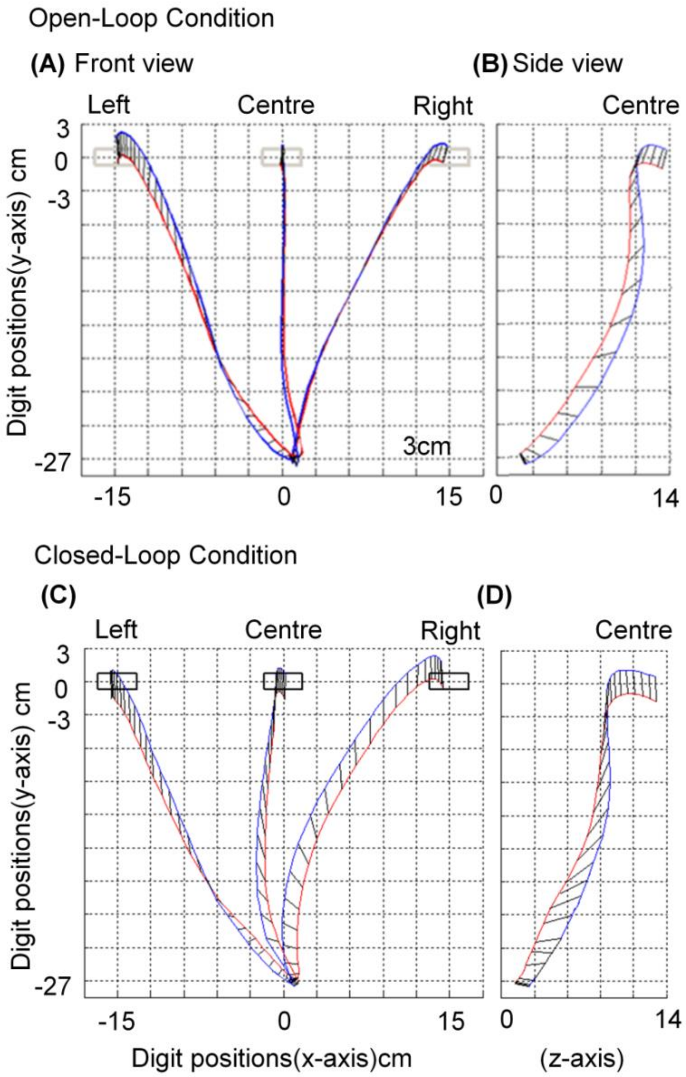

Figure 6 – Shows examples of a subject reaching to grasp horizontal targets located in the three locations in an open-loop condition (top panels: A, B) and closed-loop condition (lower panels: C, D). A and C show the changes of the thumb (red line) and index finger (blue line) positions every 20ms; the final positions of both digits were plotted on the vertical-axis as a function of the horizontal-axis every 20ms. The small black lines connecting the digit positions represent the grasp amplitude and orientation (the line connects the positions of thumb and index finger). The trajectory shows the movement trace from the starting position until the subject made contact with the screen. B and D show the central target of the same trial with the same subject from the lateral view. The positions of the thumb and index finger were plotted on the vertical as a function of the forward-axis (toward the screen).

This was followed by a final adjustment period in which the thumb-finger line was oriented roughly orthogonal to the stimulus, and hand position was advanced forward by several centimeters (Figure 6B) to contact the stimulus screen. Very similar observations were made in the closed-loop condition (Figure 6C, D) except that we noted a trend (not quantified here) for subjects to undershoot, slow slightly, and adjust reach location toward the end of the trial. These general observations held for most trials in all subjects, but are not further quantified here.

3.2. Observed Grasp Performance

Figure 7 illustrates the accuracy and variability of participants' actual performance in the open-loop (left column; A, B) and closed-loop (right column; C, D) conditions across both stimulus location and gaze direction. The vertical and horizontal spatial locations of the final tips of the thumb and index finger positions were plotted in centimeters on 2D Cartesian coordinates. The line between the final tips' positions shows the grasp location and amplitude with respect to reach stimulus location. The angle of the line represents the grasp orientation relative to reach stimulus orientation. The sub panels of each section (A1-9, B1-9, C1-9, and D1-9) are organized according to both target location (left, centre, and right columns) and gaze direction (top, middle, and bottom rows) as illustrated by the schematic figures placed in Figure 7A.

Figure 7A shows the grasp parameters of an example participant reaching to grasp horizontal targets in the open-loop condition. The individual trials (shown as lines joining thumb and index finger positions) demonstrate that the subject was generally able to place the hand near the centre of the stimulus, with relatively adequate grip amplitude,

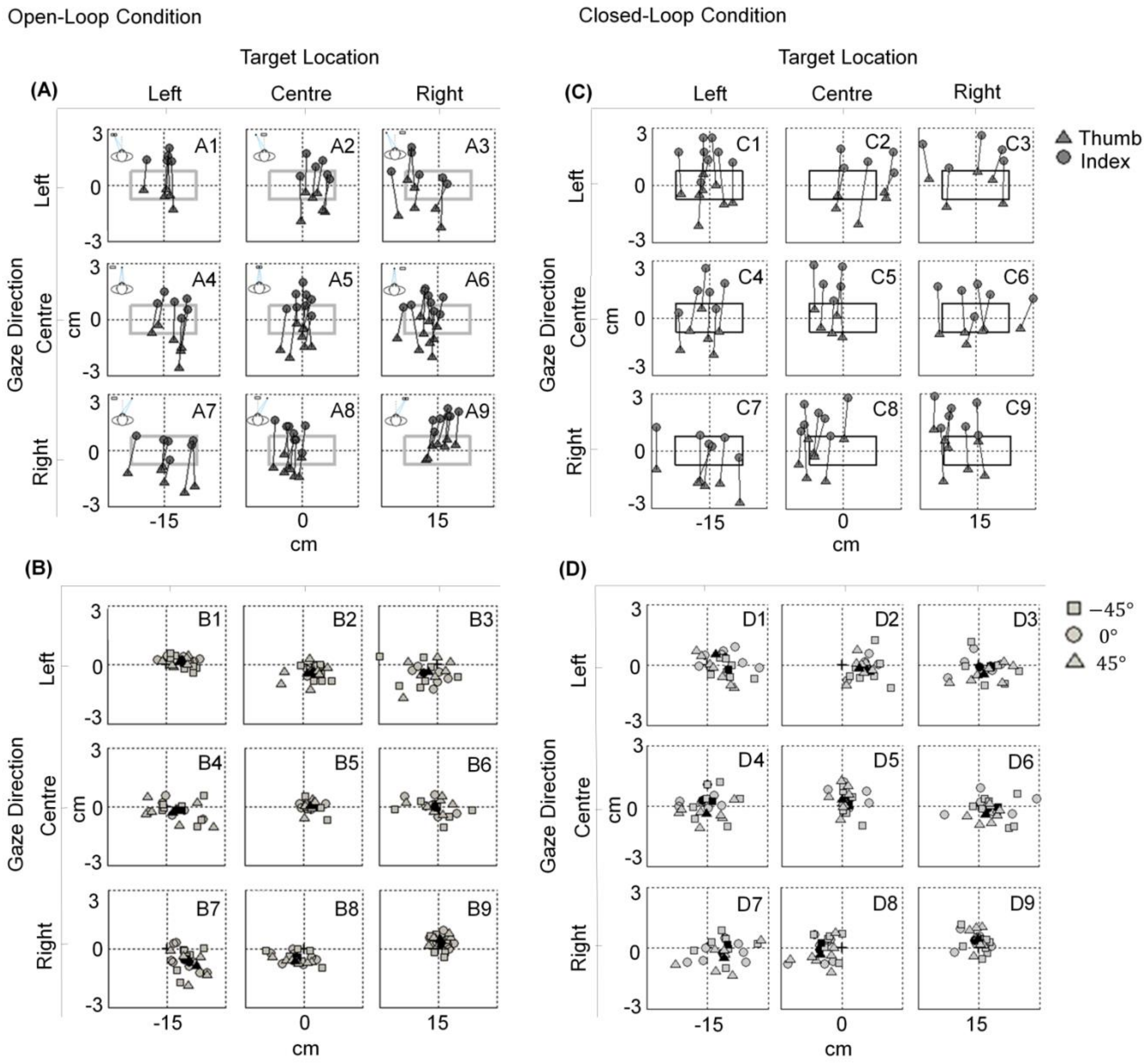

Figure 7 – Sections A and C show the final positions of grasp parameters for an example subject. The grasp parameters were plotted relative to stimulus location (vertical sub panels) and gaze direction (horizontal sub panels) in open (left section: A) and closed (right section: C) loop conditions. Each sub panel shows the vertical and horizontal spatial location (on 2D Cartesian coordinates) of the final position of the tips of thumb and index finger, and a line connecting the tips of the two digits. The angle of the lines illustrates the observed grasp orientation. The small schematics in the top left corner of the panels in section A represent the stimulus location relative to gaze. As illustrated by the small schematic, the sub panels of each section (A1-9, B1-9, C1-9, D1-9) are organized according to both target location (left, centre, and right columns) and gaze direction (top, middle, and bottom rows). According to this organization, the sub panels numbered 1, 5, and 9 (the diagonal sub panels of each section) show the trials where

subjects gazed at targets. Sections B and D show the individual mean of grasp locations (centre points of the thumb-finger lines shown in A and C) for the seven participants (gray symbols) and the averages across participants (black symbols). The data are separated according to the stimulus orientation (□ for−45°, ○ for horizontal, and △ for 45°).

and with grasp oriented orthogonally to stimulus orientation. However, both location and orientation show considerable variability. The tightest clustering appears to occur along the diagonal of the panels (A1, A5, and A9) where gaze was on the targets.

Figure 7C shows the grasp parameters in the closed-loop condition (for the same participant presented in A). Here the subject was able to clearly see the target and the subject's hand, although other background information remained very dimly visible if at all. The individual trials were similar but perhaps surprisingly more variable (less tightly clustered) from trial to trial compared to those described above for the open-loop condition.

Figure 7B shows the individual mean of grasp locations (centre points of the lines) for the seven participants (gray symbols) and averages across participants (black symbols). The data have been separated according to stimulus orientation (□ for −45°, ● for horizontal, and △ for 45°). The black symbols clustering almost on the same sites across all panels indicates that the average grasp location was not influenced by target orientation.

There was variability in the patterns of average grasp location for individual subjects, but the influence of gaze direction was clear for the average of all subjects. However, Figure 7 illustrates several other trends that will be quantified further in the text: better clustering of data across subjects occurred when the gaze was at the stimulus (B1, B5, B9); a tendency to undershoot the centre of leftward stimuli (B1, B4, B7); and a trend for reaches to shift opposite to gaze for the centre stimulus (B2, B5, B8).

Figure 7D shows the mean of reach locations across subjects in the close-loop condition. The data shows some of the same trends as those described above for the open-loop condition; for example: 1) the overall means across subjects (black symbols) undershot the centre of the centre stimulus relative to gaze direction (D2, D5, D8); and 2) the means across subjects (grey symbols) were more tightly clustered when gaze was at the target (D1, D5, D9) compared to the other gaze/stimulus combinations (quantitative comparisons between these two tasks will be provided in separate figures).

Figure 8 illustrates grasp performance when subjects reached to grasp in the open-loop (A, B) and closed-loop (C, D) conditions. The top panels (A, C) show individual trials from an exemplary subject reaching-and-grasping foveated targets oriented horizontally and tilted clockwise and counterclockwise. The sub panels (A1-9, B1-9, C1-9, and D1-9) are organized according to both target location (left, centre, and right columns) and target orientation (top, middle, and bottom rows). The bottom panels in Figure 8 (B, D) show the mean across subjects of grasp orientations and grip amplitudes after separating the data by gaze direction (illustrated by the lines connecting the digit tips). Both the individual examples and across-subject means illustrated that subjects generally oriented grasp orthogonally to the stimulus.

The example subject data (Figure 8: A, C) further suggest that the main source of variability was in grasp location (described above) as opposed to grasp orientation. Likewise, the cross-subject means (Figure 8: B, D) show a clear influence of gaze on grasp location (described above), but relatively subtle influences on grasp orientation and grip amplitude. General observations about actual grasp performance are quantified below in more detail for individual grasp parameters.

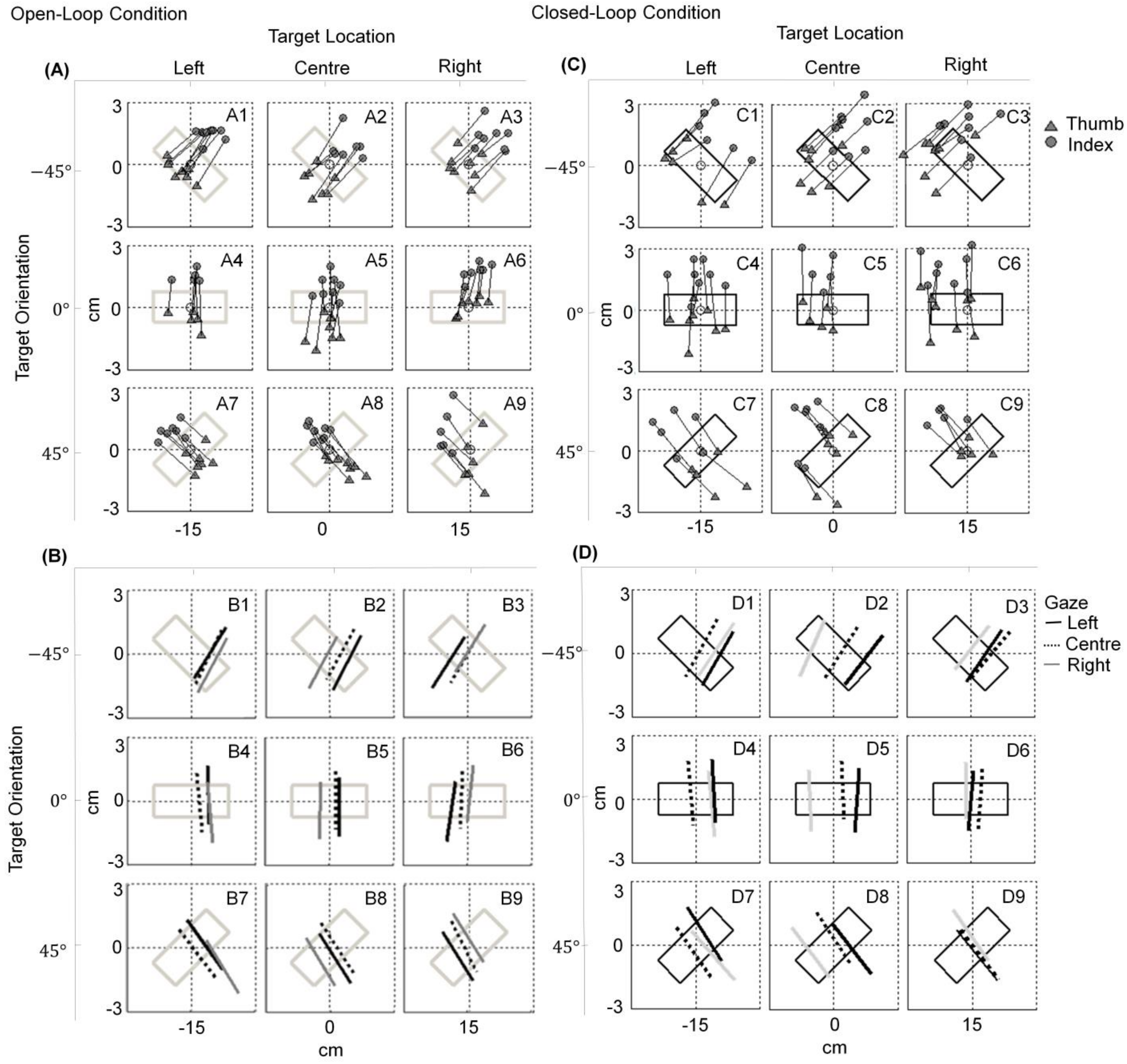

Figure 8 – The upper sections (A, C) show the observed grasp parameters (as specified in Figure 7A) for an example subject reaching to grasp foveated targets across the three different locations (left, centre, and right columns) and orientations (top, middle, and bottom rows). Sections B and D at the bottom show the average of observed grasp parameters across subjects relative to target locations and orientations and separated by gaze directions. The left column (A, B) represents the results for the open-loop condition, and the right column (C, D) shows the results for the closed-loop condition.

A mixed model analysis revealed several main and interaction effects for reach stimulus orientation, stimulus location, gaze direction, and VF conditions on the systemic and variable of grasp parameters (Table 1 shows the main effects of these parameters and Table 2 shows the interaction effects.)

3.3. Grasp Location

Figure 9 provides a general quantitative overview of grasp location deviations. The left panels (A1, A2) show the Sys-GDC, and the right panels (B1, B2) show the Var-GDC. The top panels (A1, B1) illustrate the main effect of gaze direction (collapsed across the different target locations and VFB conditions), and the bottom panels (A2, B2) illustrate the main effect of reach stimulus location (collapsed across gaze directions and VFB conditions) on GDC.

As Figure 9 shows, participants generally produced more accurate grasp location when they either gazed at (A1) or reached to (A2) a right stimulus. The systemic grasp location deviations increased slightly (overshot) for reaches towards the central position (midline); these deviations were not significantly different from rightward reaches. However, GDC deviations increased significantly for leftward reaches; the subjects undershot leftward targets.

A mixed model analysis showed main effects for stimulus location ($F\ (2{,}43.6) = 11.71,\ p \leq .001$) and for gaze direction ($F\ (2{,}39.22) = 4.37,\ p \leq .02$) on Sys-GDC. In contrast, the Var-GDC was significantly less for the central target vs. peripheral targets (Figure 9 B2). A mixed model analysis showed a main effect for reach stimulus ($F(2{,}45.20) = 6.34,\ p \leq .004$), and there was no main effect for gaze direction on the Var-GDC.

Table 1: The Main Effects of Gaze Direction, Target Properties (Orientation and Position), and VFB on the Systemic and Variable Grasp Parameters

	Target Orientation	**Target Location**	**Gaze Direction**	**VFB**
Sys-GDC	F (2,12)=1.52, p=0.26	F(2,43.6)= 11.71, p≤.001	F(2,39.22)= 4.37, p=.019	F(1,6)=.34, p=.58
Var-GDC	F(2,54.13)= 2.34, p=0.12	F(2,45.20)= 6.34, p≤.004	F(2,23.65)= 1.52, p=.244	F(1,6.01)=8.77, p=.025
Sys-Grip Amplitude	F(2,12)=0.74, p=0.51	F(2,37.79)= 1.03, p=.37	F(2,23.29)= 1.13, p=.34	F(1,15.84)= 3.30, p=.88
Var-Grip Amplitude	F(2,11.4)=1.34, p=0.31	F(2,10.32)=.51, p=.52	F(2,40.36)= 1.01, p=.37	F(1,5.84)=.58, p=.48
Sys-GAO	F(2,17.45)= 10.32, p≤.001	F(2,12.73)= 4.14, p=.041	F(2,29.59)=.88, p=.43	F(1,19.18)=.33, p=.57
Var-GAO	F(2,31.05)= 1.59, p=.16	F(2,11.86)=.33, p=.73	F(2,108.32)= 1.23, p=.31	F(1,6)=2.08, p=.20

Table 2: The Interaction Effects of Gaze Direction, Target Position, and VFB Conditions on the Systemic and Variable Grasp Parameters

	Target vs. Gaze	**Target vs. VFB**	**Gaze vs. VFB**	**Target vs. Gaze vs. VFB**
Sys-GDC	F(4,42.47)= 14.58, p≤.001	F(2,13.2)= 22.38, p≤.001	F(2,16.83)= 18.57, p≤.001	F(4,20.79)=5.6, p≤.003
Var-GDC	F(4,38.18)= 44.55, p≤.001	F(2,82.82)= 0.72, p=0.49	F(2,20.85)= 1.49, p=0.25	F(4,110.09)= 7.24, p≤.001
Sys-Grip Amplitude	F(4,40.14)= 4.65, p≤.004	F(2,15.86)= 0.64, p=0.54	F(2,108)=0.24, p=0.78	F(4,108)=0.47, p=0.76
Var-Grip Amplitude	F(4,26.99)= 3.29, p=.03	F(2,12.52)= 0.63, p=0.55	F(2,160.7)= 1.28, p=0.28	F(4,152.35)= 1.09, p=0.36
Sys-GAO	F(4,48.86)= 0.65, p=.63	F(2,30.04)= 0.18, p=0.84	F(2,17.71)= 2.49, p=0.11	F(4,41.33)= 1.74, p=0.161
Var-GAO	F(4,108.32)= 3.18,p=.016	F(2,140.7)= .654, p=0.52	F(2,140.7)= 1.05, p=0.35	F(4,140.71)= 1.67, p=0.16

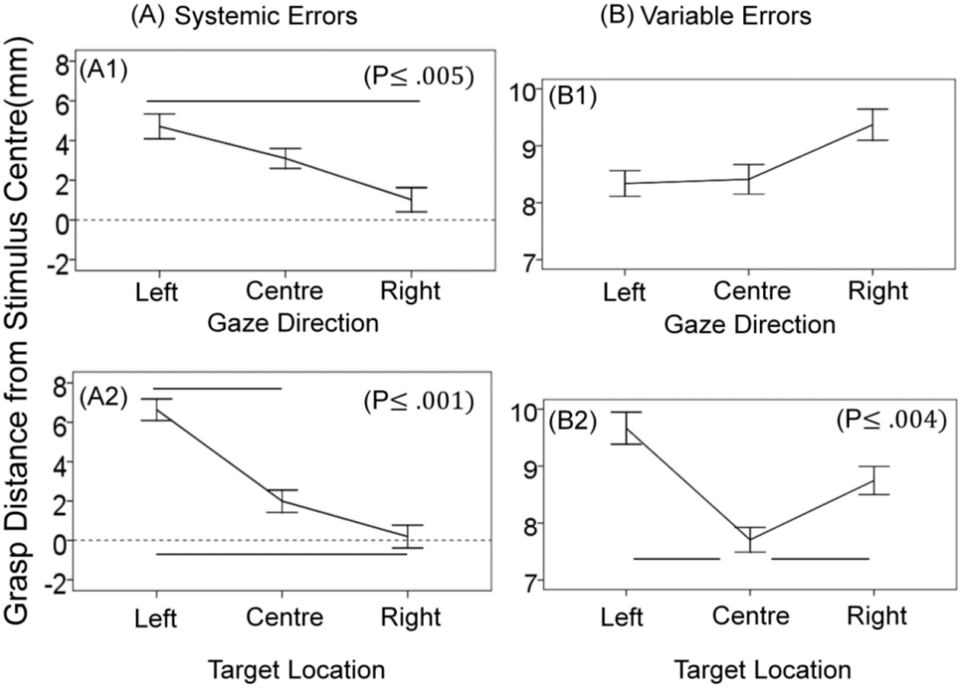

Figure 9 – The main effects of gaze and reach stimuli on grasp location deviations. Here we show the systemic (left panels: A) and variable (right panel: B) GDC (average ± SE). The upper panels (A1, B1) show the data as a function of gaze direction, collapsed across the different target locations and VFB conditions. The bottom panels (A2, B2) display the data as a function of target location (collapsed the data across the different gaze directions and VFB conditions).

Figure 10 provides a general quantitative overview of Sys-GDC (left panels: A, C) and Var-GDC (right panels: B, D) contrasting the open- and closed-loop conditions. The top panels (A, B) show these data as a function of gaze direction (collapsed across the different target locations), and the bottom panels (C, D) plot the data as a function of target location (collapsed across gaze directions).

Figure 10 shows that the Sys-GDC was relatively low and similar for both VFB conditions at central gaze (A) and central target locations (C), but showed deviations when either gaze or reach was shifted to the periphery. Gaze direction had more influence on the Sys-GDC in the closed-loop condition (A) (producing deviations opposite to gaze direction), whereas target location had more influence on the Sys-GDC in the open-loop condition (producing deviations toward centre).

A linear mixed model statistical analysis revealed an interaction effect of VFB conditions and reach stimulus locations ($F(2{,}13.2) = 22.38,\ p \leq .001$). In open-loop data (the gray line on Figure 10 C), the Sys-GDC was significantly affected by all three target locations ($p \leq .007$). However, in closed-loop conditions (the black line, Figure 10 C), the Sys-GDC was significantly different for only left vs. central target positions ($p \leq .018$).

As Figure 10A shows, there was an interaction effect of VFB conditions and gaze direction ($F(2,\ 16.83) = 18.57,\ p \leq .001$). The Sys-GDC was significantly affected by all three gaze directions ($p \leq .013$) in closed-loop conditions (the black line, Figure 10 A). However, there was no significant effect of gaze direction ($p \geq .83$) in open-loop conditions (the gray line, Figure 10A). Our results indicate that the interaction of visual inputs, gaze, and reach plays a role in the accuracy of grasp location deviations.

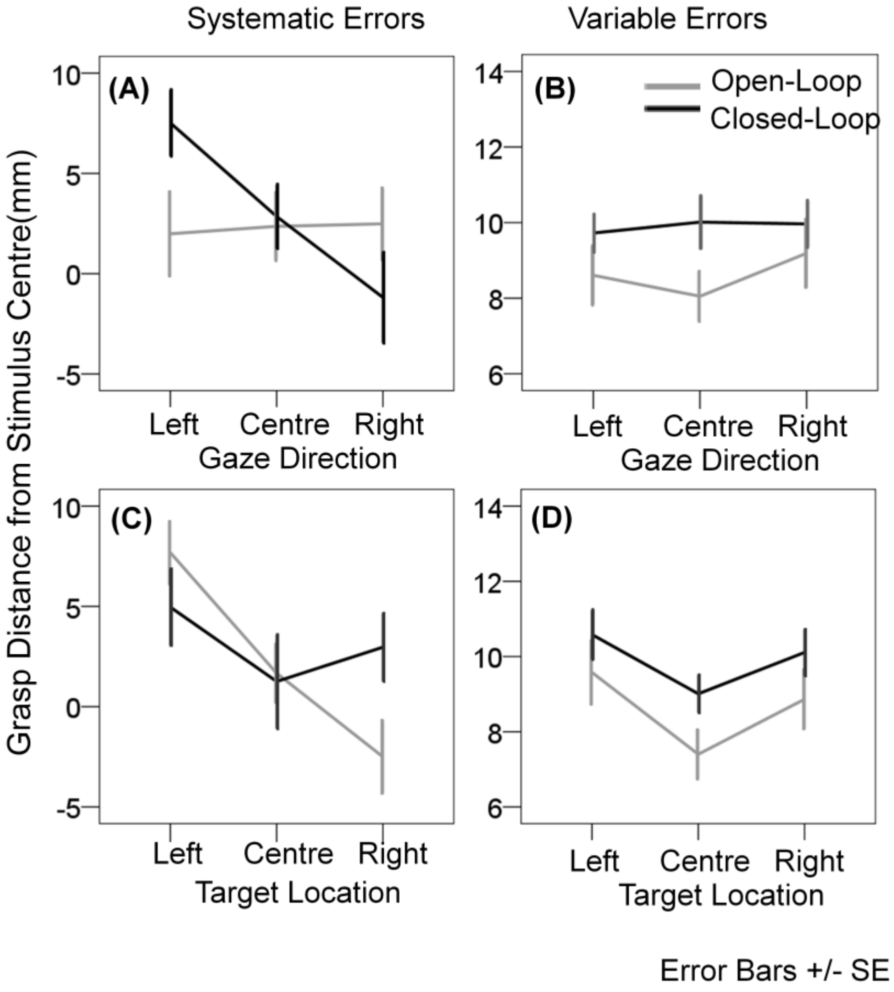

Figure 10 – Shows the interaction effects of either gaze (A) or target (C) and VFB on the horizontal GDC across subjects (average ± SE). The left panels (A, C) show the systemic GDC, and the right panels (B, D) display the variability of GDC for open-loop (gray line) and closed-loop (black line) conditions. The top panels (A, B) plot the data as a function of gaze (collapsed across the different target locations), and the bottom panels (C, D) plot the data as a function of target location (collapsing across gaze). The Y-axis in A and C shows the horizontal deviations relative to the target centre; zero is the centre of the target; values close to zero indicate an accurate grasp location; positive values indicate deviations to the right, whereas negative values indicate deviations to the left of the target centre.

The Var-GDC plotted in the left panels (B, D) of Figure 10 show two observations: 1) as noted above (in Figures 7 and 8), the Var-GDC was larger in closed-loop conditions, and 2) there was a trend for central gaze and reach position to produce lower variation, especially with respect to reach directions in the open-loop condition. Statistical analysis showed main effects for visual feedback ($F\ (1,\ 6.01)\ = 8.77,\ p \leq .025$). As stated previously, the variability of grasp location generally increased in the closed-loop condition.

A limitation in the analysis shown in Figure 10 is that it ignores interactions between gaze position and stimulus location. In fact, these interaction effects were numerous and complex. Statistical analysis revealed interaction effects of gaze and reach stimuli on the systemic ($F(4, 42.47) = 14.58,\ p \leq .001$) and variable $(4, 38.18) = 44.55, p \leq .001)$ GDC. These interaction effects may represent the relative position of target and gaze in the retinotopic map. Therefore, they may be best explained in the gaze-centred coordinate. Because there was an interaction effect of reach, gaze, and VFB conditions on the systemic ($F(4,\ 20.79) = 5.61,\ p \leq .003$) and variable ($F(4, 110.1) = 7.24,\ p \leq .001$) GDC, it is better to explain the relation of gaze and reach stimuli within each visual condition.

To study the interaction effects of gaze, reach, and VFB, we plotted the results while separating these factors. Figure 11 shows the average of Sys-GDC for open- and closed-loop conditions, but this time plotting GDC as a function of gaze separately for each target (top row), GDC as a function of stimulus location in space separately for each gaze direction (middle row), and GDC as a function of target displacement from gaze direction (bottom row) separately for each target position in space.

Figure 11 shows the typical gaze-centred overshoot pattern reported previously for pointing and reach-to-touch studies (e.g., Bock, 1986; Henriques et al., 1998, Dessing et al., 2012), but only for the central target and in both VFB conditions (as noted before in Figure 7 middle columns in B and D). Participants produced overshoot deviations opposite to gaze direction when they viewed targets from the periphery. In the open-loop condition, the Sys-GDC was significant for gazing at the target vs. rightward ($p = .002$), and gazing rightward vs. leftward ($p = .001$); in the closed-loop condition, the Sys-GDC was significant for the three gaze directions ($p \leq .001$), (see Figure 11, the dotted lines on A1 vs. B1).

Figure 11 shows that participants consistently undershot the centre of leftward targets regardless of gaze direction in both VFB conditions (as illustrated before in the left column of Figure 7B, D). However, it seems that gaze direction slightly modulates the magnitude of these deviations. In the open-loop condition, participants undershot the centre of leftward targets. The Sys-GDC was significantly less for the central gaze direction ($p = .02$) vs. right (black line in Figure 11 A1). In the closed-loop condition, the GDC for the left stimulus location decreased (close to zero) when the gaze was directed at the central stimulus ($p \leq .003$), as illustrated by the black line in Figure 11 B1.

The data showed gaze-centred undershoot for the right stimulus location in both VFB conditions (right columns on Figure 7B, D). In the open-loop condition, participants produced the most accurate grasp location when they looked at and reached-to-grasp the rightward stimulus. They produced undershoot deviations when they looked at the leftmost from the rightward reach stimulus, (Figure 11 A2).

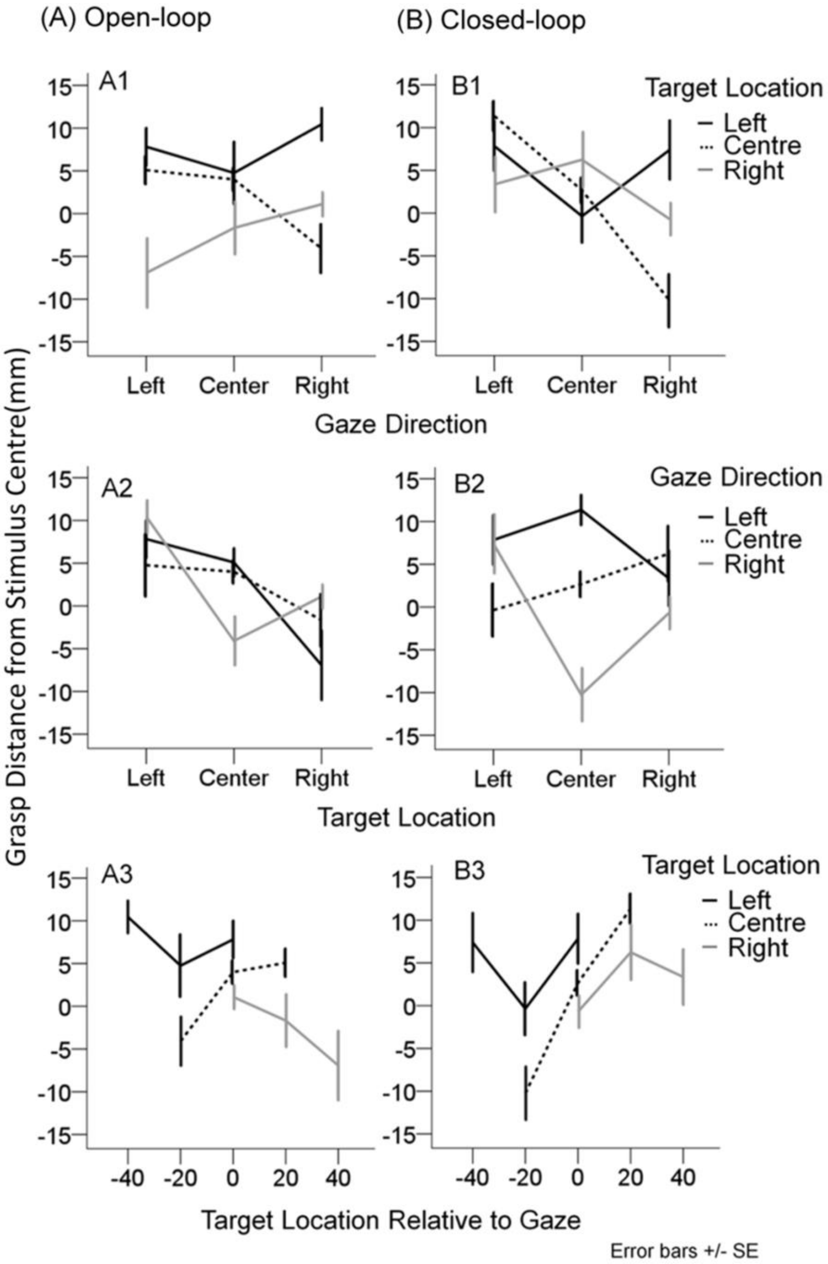

Figure 11 – The interaction effects of gaze and reach stimulus positions on the systemic GDC. Here we show the systemic GDC for open-loop (left panels, A) and closed-loop (right panels, B) conditions. The top panels show the data as a function of gaze separately for each target. The middle panels illustrate the GDC as a function of stimulus location in space for each gaze direction. The bottom panels display the same data but this time as a function of target distance relative to gaze, with the data separated by target location.

However, in the closed-loop condition, the hand and target VFB changed the pattern of GDC. Participants produced overshoot deviations when they shifted their gaze to the left (Figure 11 B2). VFB about the target and the hand imposed several modulations on the Sys-GDC. Furthermore, the VFB influences on the Sys-GDC depended on the positions of the reach and gaze stimuli in space. For example, although participants undershot the leftward stimulus, systemic deviations decreased in the presence of hand and target VFB.

Interestingly, the central gaze position reduced the Sys-GDC more than foveating the target (the black line on Figure 11 A3 vs. B3). Even though both VFB conditions showed a gaze-centred overshoot pattern for the central stimuli, hand and target VFB intensified the overshoot effects (the dotted line on A3 vs. B3 in Figure 11). Although the rightward stimulus produced the most accurate grasp location independent, the gaze-centred deviations were flipped vertically in the closed-loop in contrast to the open-loop condition (the gray line, Figure 11 A3 vs. B3). The interaction impacts of gaze, reach, and VFB were complicated. As a result of this complexity, the systemic deviations in neither the open-loop (A3) nor the closed-loop (B3) condition aligned across targets when the data were represented in gaze-centred coordinates, in contrast to the previous pointing task study (Henriques et al., 1998).

Figure 12 shows the average of the Var-GDC for open- and closed-loop conditions. Figure 12 was plotted with the same assembly as Figure 11. In contrast to the complexity seen in the Sys-GDC, the variable data followed a relatively simple pattern. At first glance at (Figure 12), it appears that the open-loop (panels A1, B1) and closed-loop data (A2, B2) show complex patterns.

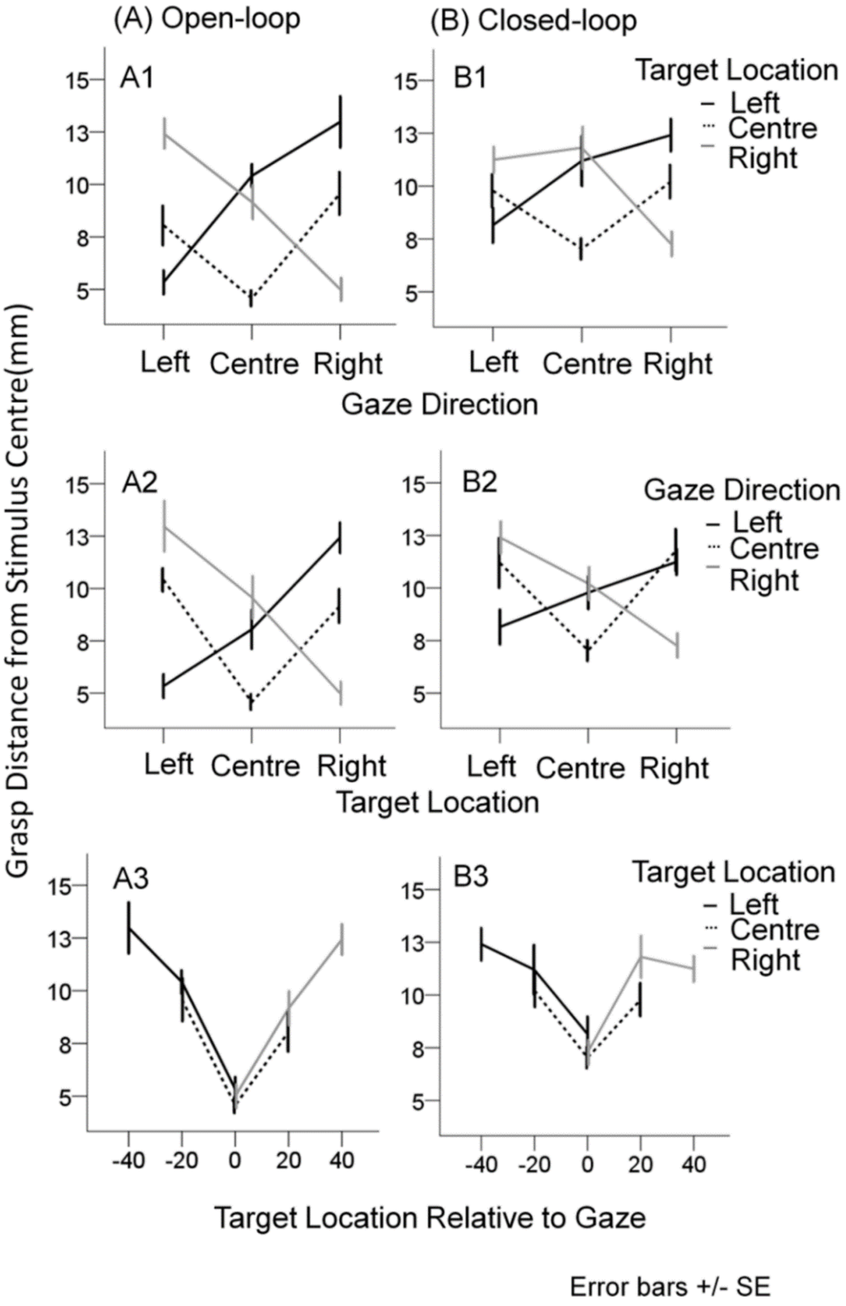

Figure 12 – The interaction effects of gaze and reach stimulus positions on the variable GDC. Here we show the variable GDC for open-loop (left panels: A) and closed-loop (right panels: B) conditions. The top panels (B, C) show the data as a function of gaze separated by target location. The middle panels illustrate the GDC as a function of stimulus location in space for each gaze direction. The bottom row shows the variable GDC in the retinal coordinate as a function of the target relative to gaze direction in the retinal coordinate.

However, when the data are plotted in gaze-centred coordinates (A3, B3), there is a simple explanation: as noted in Figure 7, the data cluster most tightly when gaze fixates the stimulus, and become more variable as the retinal distance of the target from the fovea increases. This is true regardless of stimulus location (as shown) or gaze direction (not shown).

Figure 12 shows the average of the Var-GDC data in open-loop (A) and closed-loop (B) conditions across subjects. The upper panels show the data as a function of gaze direction stimuli; the data was separated by target location (A1, B1). The middle panels (A2, B2) show the same data plotted as a function of stimulus location and separated by gaze direction. The lower panels (A3, B3) show the same data plotted as a function of stimulus location relative to gaze and separated by stimulus location.

Unlike the Sys-GDC data (represented in Figure 11 A1 vs. A2), the pattern of gaze and reach impacts on the Var-GDC were relatively the same in both panels (Figure 12 A1 vs.A2); gaze and reach directions had no direct influence on the results. However, the visual angle between gaze and reach stimuli positions strongly influenced the variability of GDC across subjects (as shown in Figure 12 A1 and A2) and for individual subjects (not shown).

Our results indicated that the variability of GDC is best presented in the eye-centred coordinate (A3). These outcomes also hold for the closed-loop data (Figure 12 B1-3). A linear mixed model analysis showed no interaction effects for gaze and VFB, and target and VFB. However, there was an interaction effect for gaze and target position ($F(4, 42.47) = 14.58, p \leq .001$). The variability of GDC increased as the magnitude (but not the direction) of the visual angle increased or as the target displacement from gaze direction increased.

Although in both VFB conditions the variability of grasp location deviations increased linearly with the visual angle (Figure 12, A3 vs. B3), the pattern was stronger in the open-loop than in the closed-loop condition. In the absence of VFB, the Var-GDC was minimal when the visual angle was zero; however, the variability sharply increased as the visual angle increased ($p \leq .001$) (figure 12 A3).

The Var-GDC in the closed-loop condition, in contrast to that in the open-loop condition, increased especially when participants foveated the targets and when gaze was directed to $(-20°)$ from the central and rightward targets (Figure 12 B2 vs. B3). However, hand and target FVB decreased the deviations for foveating the targets $(p = .002)$ vs. viewing the target from the periphery. There was no significant difference between gaze shifted to $-20°$ vs. $-40°$ from the rightward targets (Figure 12 B3). Statistical analysis showed an interaction effect of gaze, target, and VFB conditions on the Var-GDC ($F(4, 110.09) = 7.24, p \leq .001$).

3.4. Grip Amplitude

Figure 13 shows the average grip amplitude in open- and closed-loop conditions (A and B, respectively) plotted as a function of gaze for individual target location (top panels), as a function of stimulus location for each gaze direction (middle row), and as a function of target distance for gaze direction for each target location (bottom row). The grip amplitude results can best be explained in the gaze-centred coordinate. Participants tended to increase their grasp size when they shifted their gaze further away from the target.

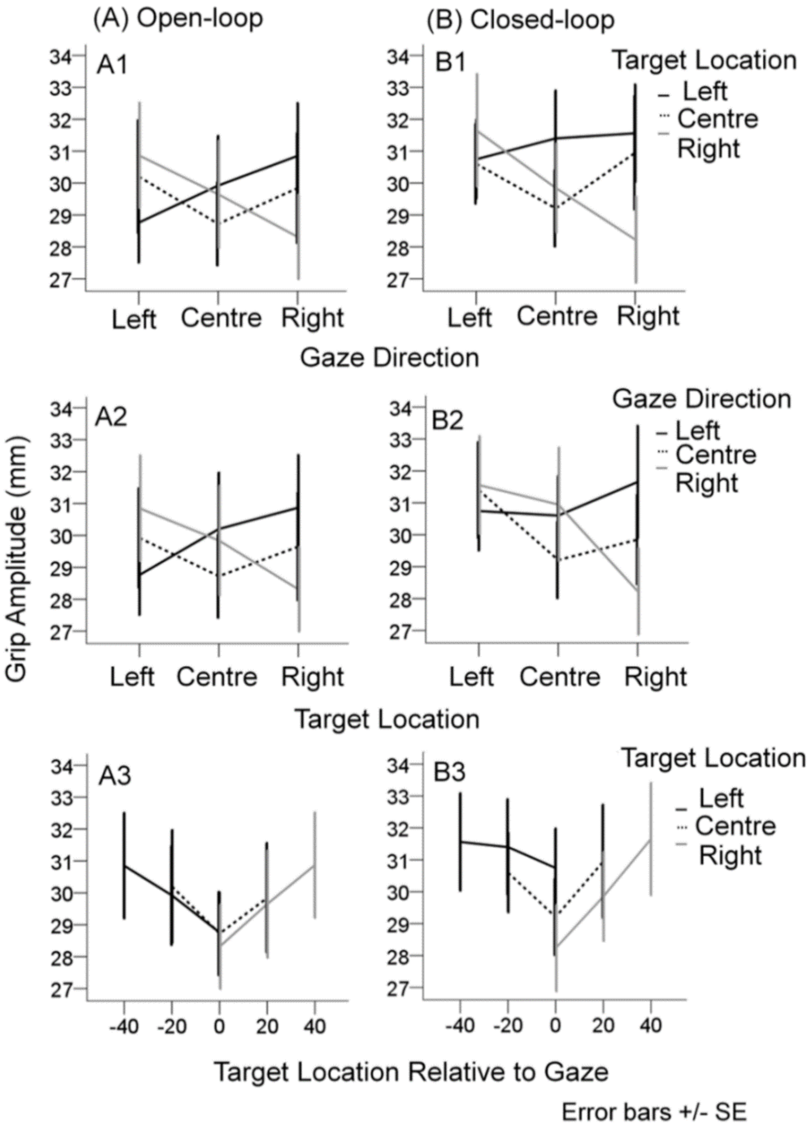

Figure 13 – Shows the interaction effects of gaze and reach stimulus positions on the average of grip amplitude. Here we show the systemic average grip amplitude for open-loop (left) and closed-loop (right) conditions. The top panels (A1, B1) shows the amplitude as a function of gaze for individual target location The middle panels (A2, B2) demonstrate the data as a function of stimulus location for the three gaze directions. The bottom panels (A3, B3) show the data as a function of target displacement from gaze for each target location.

A linear mixed model analysis revealed interaction effects for gaze and target position ($F\ (4,\ 40.14) = 4.65,\ p = .004$). However, the interaction effect of gaze reached a significant level only for targets located at the right while the subject was gazing at the leftmost (-40°) vs. foveating the rightward reach stimulus ($p \leq .001$). Although the VFB condition had no main or interaction effects on the average grip amplitude, in the open-loop condition, the data tended to overlap well in a gaze-centred coordinate, and there was a relative symmetrical pattern between left and right reach stimulus positions (Figure 13 A3).

Participants tended to increase their grip amplitude as a function of visual angle. In contrast, the closed-loop data did not overlap clearly in gaze-centred coordinates as did the open-loop data; thus, deviations towards rightward and leftward reach stimulus positions showed an asymmetrical pattern (Figure 13 A3 vs. B3). The interaction effect of gaze was revealed clearly for the right target; the grasp amplitude decreased ($p \leq .001$) when participants foveated the rightward target vs. when they gazed on the leftmost (-40°) fixating dot.

Figure 14 shows the variability of grip amplitude across subjects in the open-loop (A1-3) and closed-loop (B1-3) conditions. Like the average grasp amplitude (Figure 13 A3, B3), the interaction effects of gaze and reach stimulus on the variability of grip amplitude ($F\ (4,\ 26.99) = 3.29,\ p = .025$) were best explained in the eye-centred coordinate; the pattern took a gaze-centred representation.

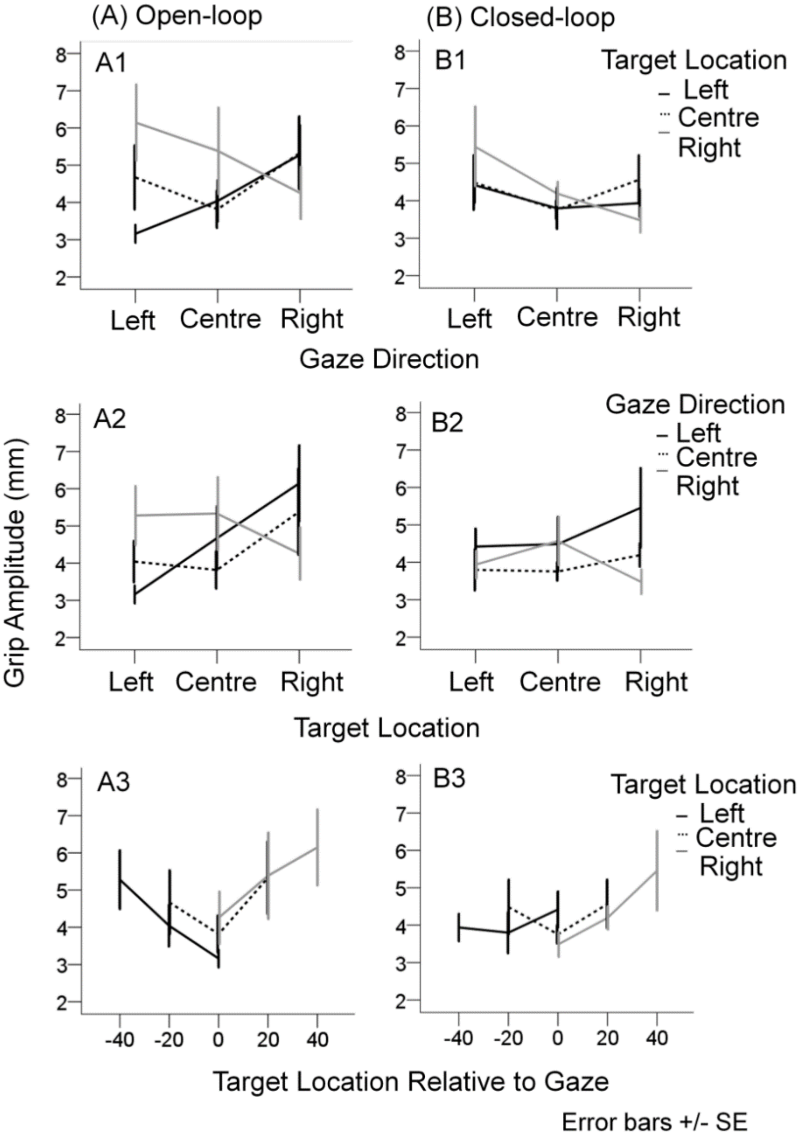

Figure 14 – Shows the interaction effects of gaze and reach stimulus positions on the variability of grip amplitude. The plots show the average standard deviation of grip size across subjects in open-loop (A) and closed-loop (B) conditions. Shadowing the previous Figure 13's schema, A1 and B1 show the variability as a function of gaze for individual target location; A2 and B2 demonstrate the data as a function of stimulus location for the gaze direction; A3 and B3 show the data as a function of target displacement relative to gaze for each target location.

Although the pattern was relatively sharper in the variable data in contrast to the average grip amplitude, gaze had significant interaction effects only for rightward targets when the subject's gaze direction was at -40° vs. looking directly at the right reach stimulus ($p = .006$).

In open-loop conditions, the variability of grip amplitude showed relatively symmetrical magnification effects for peripheral targets. In closed-loop conditions, this pattern was asymmetrical. Moreover, VFB had no effect on the variability of grip amplitude even though it appears that the variability of grip amplitude generally decreased in closed-loop conditions (see Figure 14).

3.5. Grasp Orientation

Figure 15 shows the observed grasp angle as a function of ideal grasp angle (the orthogonal angle of target orientation) for open-loop (A) and closed-loop (B) conditions, collapsing the data from all stimulus locations and gaze directions. Gray lines illustrate the average for individual subjects (± SD), and black lines show the average across subjects (±SE). As noted previously in Figure 8, Figure 15 illustrates that the observed grasp angle was linearly correlated with the ideal grasp angle in both VFB conditions.

Participants grasped horizontal targets more accurately than they grasped tilted targets. A mixed linear model analysis showed that GAO was significantly modulated by target orientation($F\ (2, 17.45) = 10.32,\ p \leq .001$). Grasp angle deviations were significantly different for targets tilted $-45°$ than for targets tilted $45°$ ($p \leq .001$) and horizontal targets ($p \leq .03$).

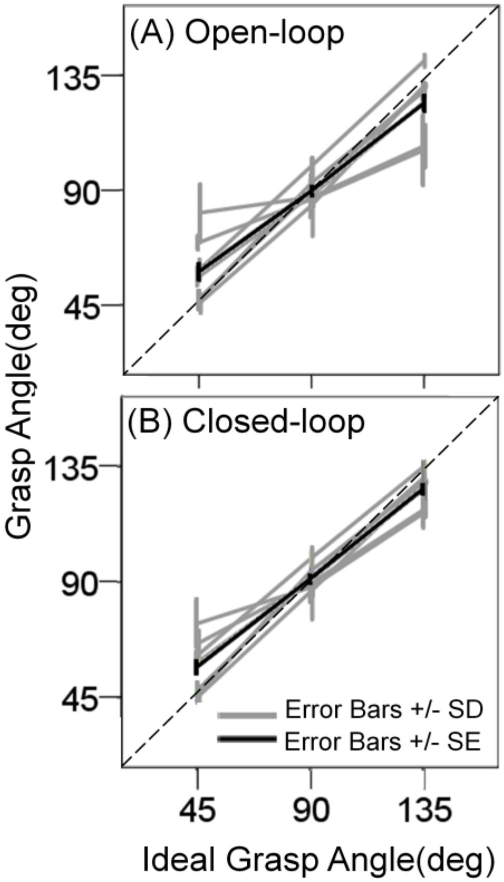

Figure 15 – Shows the average of observed grasp orientation as a function of ideal grasp angle (collapsing across the different gaze and reach positions) for individual subjects (average ±SD) (shown as gray lines) and across subjects (average ±SE) (black lines). The top panel (A) shows the data for open-loop, and the bottom panel (B) demonstrates closed-loop data. The ideal grasp angle is the orthogonal angle of target orientation (target orientation + 90°).

However, there was no significant difference between GAO for targets oriented $45°$ vs. $0°$. Consistent with this, the intercept indicates an offset nearly orthogonal to the stimulus; the average grasp orientation angle from orthogonal (GAO) was close to zero for the horizontal stimulus in both VFB. The slope indicates an "undershoot" of grasp angle for the tilted stimulus ($grasp\ angle = 0.76\ (stimulus\ angle) +\ 90.44°,\ R^2 = 0.74$ in open-loop, and $grasp\ angle = 0.8\ (stimulus\ angle) +\ 91.16°,\ R^2 = 0.84$ in closed-loop conditions).

Figure 16 quantifies the Sys-GAO for the open-loop (A) and closed-loop (B) condition as a function of stimulus orientation. These data are plotted separately for gaze direction (A1, B1) and stimulus location (A2, B2). Figure 16 shows the undershoot effects clearly for tilted stimuli (noted in Figure 15), as well as showing that the Sys-GAO was influenced by target location especially for the horizontal stimuli (A2, B2). A linear mixed model analysis showed a significant effect for target location on the Sys-GAO ($F(2, 12.73) = 4.14,\ p = .04$. The Sys-GOA significantly differed for rightward stimulus ($p = .013$) from leftward stimulus positions.

For targets tilted$-45°$, participants undershot the ideal angle with relatively smaller deviations ($\approx 9°$) for rightward than for leftward targets ($\approx 15°$); for horizontal targets, participants undershot the ideal angle ($\approx 3°$) for rightward stimuli, and overshot the angle ($\approx 4°$) for stimuli located on the left; for targets tilted $45°$, participants undershot the ideal angle with lesser deviations ($\approx 9°$) for left than right target positions ($\approx 11°$). Central targets always tended to produce midway deviations (≈13°, $0.1°$, and 10°, for $-45°$, 0°, and 45° oriented stimuli, respectively).

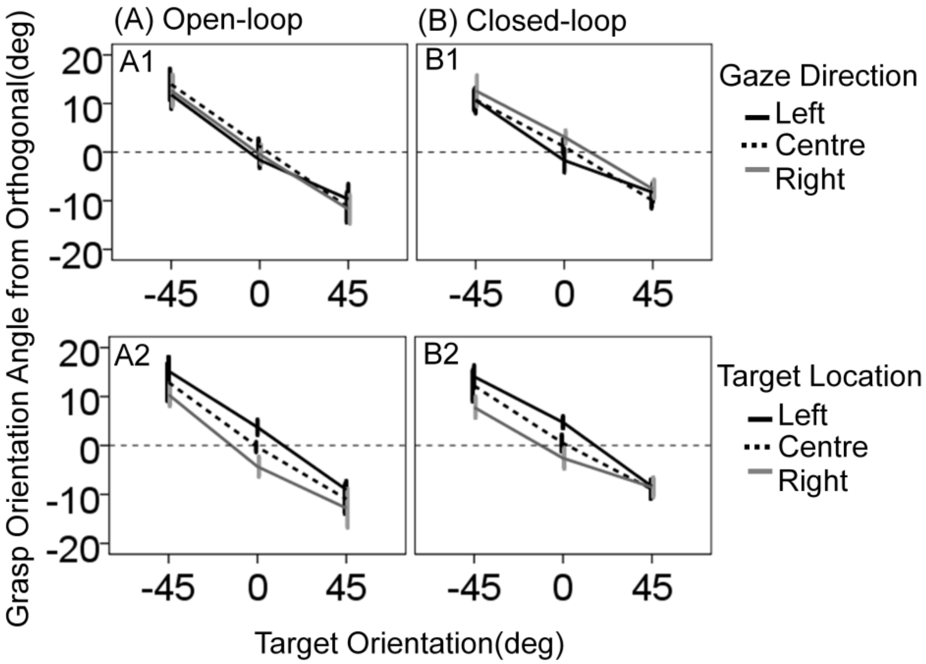

Figure 16 – Shows the systemic GOA (average across subjects ± SE) for open-loop (left panels: A) and closed-loop (right panels: B) conditions as a function of reach stimulus orientation. The top panels (A1, B1) plot the data for each gaze direction (collapsing across target locations); the bottom panels (A2, B2) plot the data for individual target location (collapsing across gaze).

The grasp angle deviations showed simple and consistent patterns; the deviations were continuously biased towards the direction of the reach stimulus.

Figure 17 shows the Sys-GOA across subjects for open-loop (top panels) and closed-loop (bottom panels) conditions as a function of target relative to gaze separated for each target position. The sub panels show the data for individual target orientation (left, middle, and right for$-45°, 0°, \text{and } 45°$, respectively). In closed-loop conditions, the data seems to be realigned in the retinal coordinate for the $45°$ and horizontally oriented targets. However, neither gaze direction ($F(2,\ 30.17) = .91,\ p = .42$) nor VFB conditions ($F\ (1,\ 18.27) = 0.49,\ p = 0.49$) had main or interaction effects on the Sys-GAO.

Figure 18 displays the variability of GAO for open-loop (A) and closed-loop (B) conditions. The upper panels (A1, B1) show the data as a function of gaze direction for individual target location; the middle panels (A2, B2) plot the data as a function of target location separated by gaze direction; and the lower panels (A3, B3) show the data as a function of target relative to gaze in the retinal coordinate.

The Var-GOA data in Figure 17 demonstrates some trends: it appears that 1) in closed-loop conditions, the Var-GOA generally decreases; 2) the Var-GOA shows magnification effects (the deviation increases as a function of visual angle); 3) the Var-GOA data is best represented in retinal coordinates (A3 vs. B3); 4) in contrast to the closed-loop condition, the magnification effects are sharper in the open-loop condition; 5) the pattern of the Var-GOA became relatively flattened and asymmetrical in the closed-loop (in contrast to the open-loop) condition especially for the left target (Figure 18, A3 vs. B3).

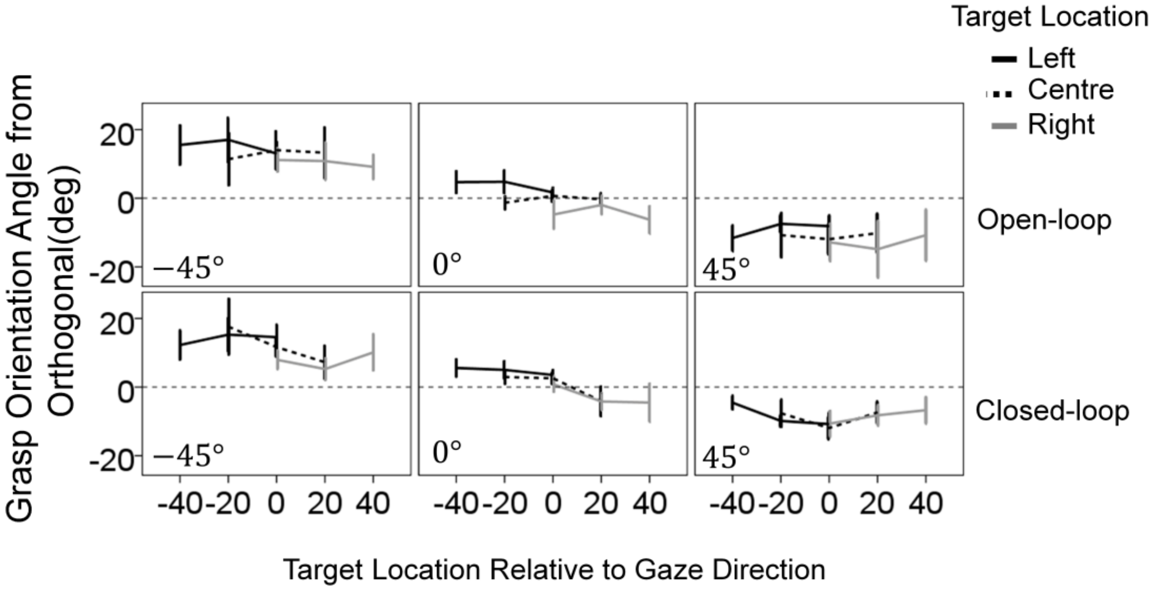

Figure 17 – Shows the systemic GOA (average across subjects ± SE) for open-loop (top panels) and closed-loop (bottom panels) conditions as a function of target relative to gaze separately for target positions. The individual panel shows the data for each target orientation (left, middle, and right for −45°, 0°, and 45°, respectively).

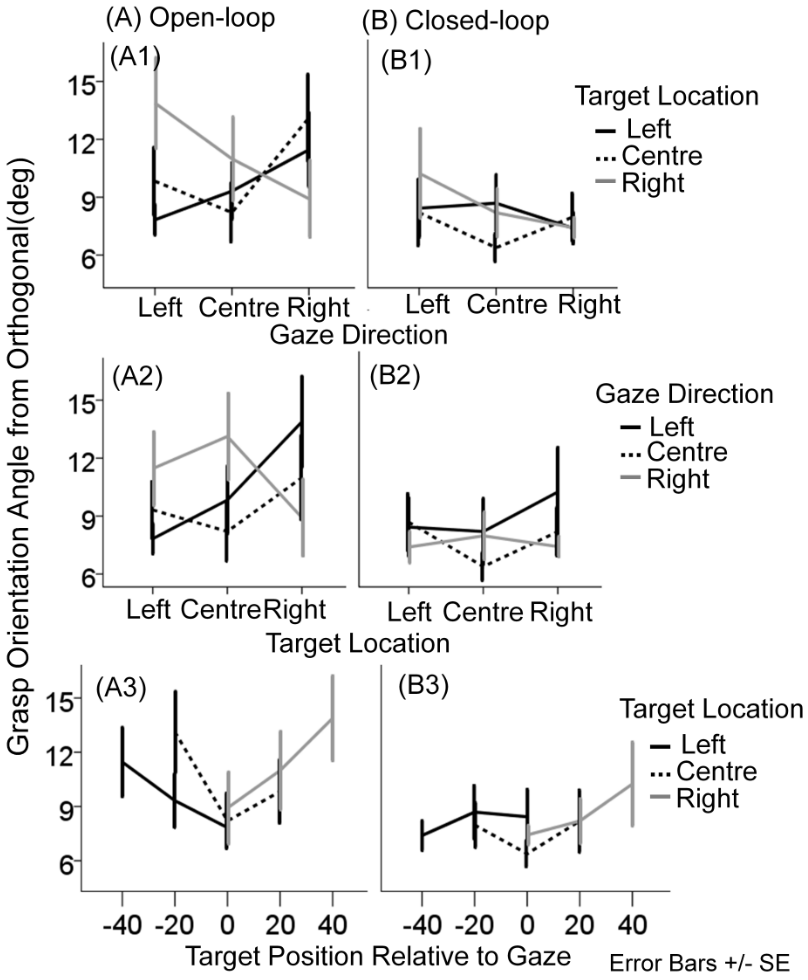

Figure 18 – Shows the interaction effects of gaze and reach stimulus positions on the variability of grasp angle deviations. The average of variable GOA across subjects is plotted for open-loop (left panels: A) and closed-loop (right panels: B) conditions. The top panels (A1, B2) illustrate the GDC as a function of stimulus location in space for each gaze direction. The middle panels (A2, B2) show the data as a function of gaze separated by target location. The bottom panels (A3, B3) show the variable GDC as a function of target relative to gaze direction in a retinal coordinate.

In closed-loop conditions, it appears (see Figure 18B) that the variability of GAO is generally decreased; however, a linear mixed model analysis revealed no significant main or interaction effects for FVB on the Var-GAO. Statistical analysis revealed a significant interaction effect of gaze and target position$(F(4, 108.32) = 3.2,\ p \leq .016)$. Figure 18 shows that gazing at targets reduces the variable GOA significantly more than viewing targets from the retinal periphery. The Var-GOA increases significantly for the left gaze direction ($p = .008$) when subjects grasped rightward stimulus, and for the right gaze direction (p=. 013) when participants grasped the central reach stimulus.

Neither grasping parameter (magnitude and orientation) was directly influenced by gaze. However, both were modulated by the interaction of gaze and reach stimulus position in space. Grasp amplitude and orientation were best represented in retinal coordinates. The accuracy and precision of grip amplitude were modulated by the visual angle, whereas the precision of grasp orientation was strongly modulated by the visual angle. Their patterns in retinal coordinates exhibited some similarity with moderate modulations (Figures 13, 14, and 18).

CHAPTER FOUR

4. DISCUSSION

The experiment was designed to investigate the effects of gaze, target, and visual feedback inputs on grasp parameters in reaching tasks. We manipulated target properties to induce more complexity in the motor action in contrast to simple pointing or reach-to-touch tasks. We tested the effects of gaze direction on the accuracy and variability of final grasp parameters towards remembered target locations and orientations. We used these quantitative results to determine 1) how increasing the properties of reach stimulus influences reach-related activity (grasp location) and grasp-related activity (grasp amplitude and orientations); 2) how gaze signals affect reach- and grasp-related activities; and 3) how VFB inputs about the hand and target affect the pattern of both reach- and grasp-related deviations. The results showed that subjects were generally able to place their hands near the centre of the stimulus, and they were able to orient their grasp orthogonal to the stimulus angle with adequate grip amplitudes.

Our results showed that both grasp location and grasp orientation deviations were influenced by stimulus positions. In general, the effects of reach stimulus position on grasp location formed a relatively simple pattern: 1) participants produced more accurate grasp location when they reached to a right stimulus; 2) systemic deviations tended to slightly increase with a central target; and 3) systemic deviations increased and subjects persistently undershot the leftward target.

The impacts of gaze direction on grasp location were dependent on target position in space. The interaction of gaze and target position revealed complex mechanisms. We found that the central and rightward stimulus showed strong gaze-centred effects, whereas the undershoot pattern was maintained for leftward targets (although shifting gaze to the central position showed some modulation on systemic GDC). The interaction of gaze and reach in a grasping task produced Sys-GDC responses that were not aligned in the eye-centred coordinate. Furthermore, the variability of gaze- and target-dependent deviations was strongly influenced by the interaction of target and gaze position in space, and these deviations were correlated linearly with the visual angle. The Var-GDC responses were represented well in the eye-centred coordinate.

Both grasping parameters (magnitude and orientation) were modulated by the interaction of gaze and reach stimulus positions in space, and the deviations were best represented in the eye-centred coordinate. The accuracy and precision of grip amplitude, as well as the precision of grasp angle patterns in the retinal coordinate, exhibited some similarity with moderate modulations. Grasp orientation was correlated linearly with target angle. However, tilted targets impacted grasp angle; horizontal stimuli produced more accurate grasp orientation than a tilted stimuli. Participants persistently undershot the ideal grasp angles for tilted stimuli. Furthermore, the direction of the grasp angle deviations was dependent on stimulus positions. The impacts of reach position on the Sys-GOA showed a consistent pattern in contrast to Sys-GDC. The direction of the systemic grasp orientation was consistently biased towards the direction of the reach stimulus position in space.

VFB about the target and the hand heavily influenced the reach component of the grasping action. VFB had no direct impact on grasp location deviations; however, VFB impacts showed as a result of VFB interaction with gaze, target, or both. We found that reach stimulus position had a stronger impact in the absence of VFB, whereas gaze direction had more effects when VFB about the hand and the target were accessible. VFB input modulations to reach- and gaze-dependent deviations revealed complex mechanisms. The results showed that VFB about the hand and the target modulated grasp location by intensifying the patterns of the systemic gaze-dependent deviations for central and left targets and by increasing the variability of grasp location deviations especially when gaze was at the target.

4.1. Grasp Location Deviations Associated with Reach Stimulus Location

Subjects made more accurate reaches when they looked at and grasped rightward targets as opposed to other stimulus locations. Our results suggested an advantage for movement made to targets located on the same side as the reaching hand. The simplest explanation for the accuracy of right reaches is that all our subjects were right-handed. Our results are consistent with previous studies that found greater endpoint accuracy for movement towards ipsilateral targets when contrasted with movement to contralateral targets (Carey et al., 1996; Hodges et al., 1997; Fisk and Goodale, 1985). The interpretation of ipsilateral accuracy is that the visual information of an ipsilateral target position is processed (at least initially) in the same hemisphere as the motor and sensory signals with direct connections to the reaching hand. The accuracy observed for right reaches could be a consequence of more efficient within-hemisphere visuomotor transformations (Hodges et al., 1997).

Our results showed undershoot effects for leftward targets, which is consistent with previous research (e.g., Paulignan et al., 1997; Selen and Medendorp, 2011; Bock and Eckmiller, 1986). Bock and Eckmiller (1986) found spatial undershoot effects for large movement displacement. The study argued that systematic errors depended on the required movement amplitude. Furthermore, in this study arm movements were constrained by a lever that pivoted around an axis close to the shoulder, and the motion was constrained to one degree of freedom.

However, the undershoot effects for leftward targets observed in this study could not be accounted for by movement amplitude relative to the hand as both left and right targets were located at the same distance relative to initial hand position. Participants made almost accurate reaches to rightward targets. Nevertheless, the undershoot effects could be related to the target distance relative to the right shoulder. Figure 9 shows that the systemic deviations of grasp locations increased as the distance of the reach stimulus location from the right shoulder increased.

The undershoot results for leftward targets could not be related to biomechanical discomforts because our data showed that there was spatial overshooting for leftward targets within and between subjects (see Figure 7). The persistent undershoot effects for the left target may be accounted for by motor control system constraints. Movement direction often affects motor output execution at the biomechanical level. The postural requirements are different for right and left reaches, especially for the upper limb structures (Paulignan et al., 1997).

Evidence has shown that patterns of muscle activity that participate in producing reach movement depend on the direction of the movement. Arm movement is biomechanically constrained because shoulder and elbow movements are tightly coupled. The angular motion at the elbow is coupled inertially with the angular motion at the shoulder. In other words, a torque produced by muscle contraction at one joint results in angular motion at both joints. The advantage of a functional relation between shoulder and elbow motions may be that some of the complexity of the control problem is reduced (Lacquaniti and Soechting, 1982).

Interaction torque is one of the biomechanical factors that influence the performance of multijoint arm movements (Dounskaia et al., 2000; Dounskaia et al., 2002). Evidence has shown that interactive torque facilitates movement execution (Gribble and Ostry, 1999). Interaction torque imposes different demands for muscular control across movement directions. For example, interaction torque was found to assist horizontal shoulder-elbow movements in the left-diagonal direction; that is, when one joint flexed, the other extended. However, the torque produced resistance to the motion in the lateral direction in which both joints simultaneously extended (Dounskaia et al., 2002; Gribble and Ostry, 1999).

4.2. Grasp Location Deviations Associated with Gaze Direction

The results showed that systemic deviations of grasp location were modulated by gaze direction, and this modulation was strongly dependent on target position in space. Our results were in agreement with other studies as far as the experimental manipulations were similar. The result for the central target was consistent with the previous findings of typical gaze-dependent overshoots (Henriques and Crawford, 2002; Medendorp and Crawford, 2002; Bock, 1986; Henriques et al., 1998).

Several studies have investigated the spatial pattern of final movement errors to determine the reference frames involved in arm movement planning. These studies have found that errors in goal-directed movements vary as a function of the position of the target relative to gaze. Evidence has shown that the spatial position of a reach stimulus is initially encoded and updated in an eye-centred frame of reference regardless of whether the stimulus is visual, auditory, or tactile (e.g., Henriques et al., 1998; Medendorp and Crawford, 2002; Van Pelt and Medendorp, 2008; Selen and Medendorp, 2011; Pouget et al., 2002; McGuire and Sabes, 2009; Cohen and Andersen, 2000).

Earlier studies found that the sources of these spatial overshoots arise during the early stages of visuomotor transformations in a frame of reference that requires gaze direction signals. Thus, target locations are coded in a retinotopic frame of reference and modulated by eye movement in a gaze-centred coordinate (Henriques et al., 1998; Medendorp and Crawford, 2002; Van Pelt and Medendorp, 2008; Selen and Medendorp, 2011). Gaze-dependent errors could not be related to early visual representations because any distortion in the early visual processing map would be linked to all motor responses (Henriques and Crawford, 2000; Henriques et al., 1998; McGuire and Sabes, 2009).

Gaze-dependent errors could arise in hand-to-target transformation in a gaze-centred coordinate (Batista et al., 1999; Beurze et al., 2006; Crawford, Henriques, and Medendorp, 2011) or in the target-to-body transformation in a body-centred coordinate (McGuire and Sabes, 2009). Thus, gaze-dependent overshoots may reflect overestimation of the target displacement relative to gaze (Bock, 1986; Henriques et al., 1998) or underestimation of gaze direction relative to the target (McGuire and Sabes, 2009). However, our results showed that systemic gaze-dependent deviations might arise from the interaction of both reach and gaze direction as a result of the involvement of an intended grasping movement.

Previous studies are consistent with a dynamic gaze-centred internal representation of reach space (e.g., Bock, 1986; Henriques et al., 1998; Crawford, Henriques, and Medendorp, 2011; Khan et al., 2002, 2005). However, several studies have shown that in the visuomotor transformation process, hand and target positions are also encoded in body-centred coordinates (Soechting and Flanders, 1989; Gordon et al.,1994; Flanders et al., 1992) or in both gaze- and body-centred coordinates (Beurze et al., 2006; Marzocchi et al., 2008; Khan et al., 2007; Battaglia-Mayer et al., 2001).

Khan et al. (2007) found that reaching errors by both control subjects and optic ataxic patients revealed an influence of target position in gaze-centred coordinates, as well as a body-centred influence on target position. These findings suggested that target and hand positions are compared in multiple reference frames at different levels, and these comparisons are then integrated during visuomotor transformations. However, it is still unclear at which stage the hand and gaze integration occur. Considerable evidence has shown that for reaching performances, the medial parieto-frontal network is involved in integrating (gradually and across different frames of reference) information about target and hand locations (Batista et al., 1999; Battaglia-Mayer et al., 2003; Burnod et al., 1999; Blohm and Crawford, 2007). Furthermore, it has been found that comparing hand-target information in multiple reference frames could be dependent on task requirements or available sensory information (Neely et al., 2008).

Directing arm movement to a visual target requires utilizing sensory signals that are initially represented in different frames of references. Furthermore, sensory inputs (specifying target location) need to be transformed into neural outputs to arm muscles. However, neural commands sent to muscles must carry both kinematics and kinetics aspects of movement. Thus, additional transformation between kinematics (movement) and kinetics (forces) are required in the mechanism that controls the arm. The motor system is required to plan the movement in joint (intrinsic) coordinates before or during movement execution, or may be parallel to kinematic planning.

The relationship between movement and force in the arm is complex. Movement and force are not co-linear during arm motion; the direction of movement is not determined by the direction of muscle force. The direction of arm movement depends on several factors including the orientation of the force vector, arm posture, angular motion of the joints, and other biomechanical factors such as muscle stiffness and intersegmental dynamics (Flanders and Soechting, 1990; Mussa-Ivaldi et al., 1985; Hollerbach and Flash, 1982). All these factors must be taken into account during the planning and execution of arm movements.

There is evidence that neurons in the motor cortex encode the direction of movement by a population vector, and this vector accurately predicts the direction of hand movements in Cartesian coordinates. The population vector matched the observed hand trajectory even when it was calculated at 20ms intervals starting 500ms before the onset of movement and continuing until 300ms after the onset of movement (Georgopoulos et al., 1988). The M1 is the best candidate to incorporate dynamics-related activity in real time during motor behavior and to integrate information about arm geometry, arm posture, mechanical factors, and the causal forces necessary to produce the desired motor output (Sergio and Kalaska, 1997, 2003; Sergio et al., 2005).

Our results showed that target eccentricity had an influence on the precision of grasp location performance. The magnification of the variable errors varied linearly as a function of visual angle rather than of eye or target position. That is, variable errors were magnified as a function of the difference between gaze and the target, and the amount of these errors was independent of the actual direction of gaze or the target. These findings suggest that variable errors might arise in the eye-centred coordinate, and these errors could be linked to visual signals from the retinal periphery.

This variability contributed to the increase of grasp location uncertainty (precision) as a function of the visual angle between gaze and target position. This uncertainty could arise from noise in the system as a result of the variability inherent in receptors, limitations in receptor density, or delays as a result of sensory feedback (for example, variability in retinal receptors provides different visual acuity, which adds uncertainty to visual feedback). Uncertainty also can arise from the inherent ambiguity in sensory processing, such as ambiguity that arises when the 3D world is projected onto the 2D on the retina (Yuille and Kersten, 2006).

The behavioural variability of the grasp location could be physiologically relevant. Evidence has shown that the precision of the action potential of a single-neuron timing scale is behaviorally relevant to perception (Carr and Konishi, 1990; Fairhall et al., 2001; Fasial et al., 2008). There is a range of variability in neurons in visual pathways. Moreover, depending on the stimulus conditions, a single neuron can respond with different amounts of variability, and high- and low-variability neurons are often observed in the same region (de Ruyter van Steveninck et al., 1997; Kara, Reinagel, and Reid, 2000; Warzecha and Egelhaaf, 1999). The presence of certain levels of noisy signals can be used by the system (Fasial et al., 2008) to control the precision of hand movement. Our results show that variability (within and across trials) was represented clearly in eye-centred coordinates and contributed to sensorimotor control processes.

4.3. The Effects of Visual Feedback on Reach and Grasp Parameters

The results showed that reach stimulus had stronger impacts in open-loop data, whereas gaze direction had more effects in closed-loop conditions. When there is no accessibility to visual inputs during the movement, the brain may rely more on proprioceptive inputs to guide the hand to the remembered location of the target. In this case, the variability was steady and dependent on reliable intrinsic sources of information (memory and proprioceptive). Evidence has shown that hand motor information plays an important role in the sensorimotor control process (Beurze et al., 2006; Boussaoud and

Wise, 1993a, b; Caminiti et al., 1991; Crammond and Kalaska, 1994; Kalaska et al., 1997; Scott et al., 1997; Scott and Kalaska, 1997; Sergio and Kalaska, 1997; Wu and Hatsopoulos, 2006). However, when VFB about the target and hand is available, the brain relies more on visual inputs to compare hand and target locations in space. The brain utilizes multimodal inputs and estimates an optimal mechanism that minimizes the errors associated with multimodal input integration. This optimization process weighs sensory signals depending on their relative precision and the context of a task demand (Sober and Sabes, 2005; Ernst and Banks, 2002; van Beers, Sittig, and Gon, 1999).

In our study, hand and target VFB increased the systemic and variable deviations of grasp location contrary to other studies that found VFB decreased movement-related errors (Buneo and Andersen, 2006; Crawford et al., 2004; Sober and Sabes, 2003, 2005; Blohm and Crawford, 2007; Paillard, 1996; Jeannerod, 1999; Desmurget et al., 1995; Rossetti et al., 1995; Dessing et al., 2012). Our results showed that the increase in grasp location deviations was not arbitrary, so it could not be related to a sort of noise or distraction caused by the light. VFB inputs about the hand and target intensified the patterns of systemic deviations. These modifications could be caused by overestimating hand size or hand distance relative to the target. That might have occurred in our experiment because the light was directed to the hand in a completely dim environment (the surroundings were covered by black sheets).

A recent study found that the brain adapts to different strategies during visuomotor control. Prime and Marotta (2013) found that participants used different visuomotor strategies to grasp remembered and visible rectangular objects. The brain tends to utilize information that is relevant to the task. During a memory guided task, the brain seems to use general perceptual analysis of the object's properties that could be used by the subsequent memory representation to plan the grasping action. In contrast, when grasping a visible target, the brain activates a visual process that may obtain specific information about the object's graspable dimensions such as direct points of contact.

4.4. Grasp Angle Deviations Associated with Target Orientation and Location

Target orientation had an impact on grasp angle deviations. The most accurate grasp was produced by a horizontal target, whereas participants undershot both tilted targets. The greater deviations were produced by the $-45°$ tilted targets. The grasp angle undershoot effects could be interpreted as motor control system constraints. The angular amplitude of joint rotation and the level of coordination between the elbow and shoulder joints were found to be affected by stimulus orientation (Dounskaia et al., 2002). The elbow and shoulder rotated anti-phase (flexing one segment while extending the other due to simultaneous activation of nonhomologous muscle groups) for a line tilted counterclockwise. Both joints coordinated in-phase (flexing or extending the arm spontaneously due to simultaneous timing of activation of homologous muscle groups) for horizontal lines. However, this study found that the shoulder amplitude was very small for a line tilted clockwise, and the movement was performed mainly by the elbow joint (Dounskaia et al., 2002).

Some studies have found that grasp orientation deviations could occur as a result of misestimates of target orientation caused by perceptual misjudgment. Dick and Hochstein (1989) tested observers' judgment towards different bar orientations. Subjects wrote down the predicted angles using a computer keyboard. They found that observers misestimated the true values of an oblique bar. Tilted bars were seen as closer to the vertical than they really were. They found no deviations for vertical and horizontal stimulus orientations (Christopher and Stephen, 2000; Tomassini, Morgan, and Solomon, 2010). A recent study argued that misestimating a target orientation occurred because of substantial biases in the very early representations and in basic visual attributes (Ahna, Landy, and Simoncelli, 2011). However, evidence has shown that vision for action within the dorsal stream is separate from vision for perceptual processing (Goodale, 2014; Goodale and Milner, 1992).

Our results showed there was a bias of grasp angle deviations toward the direction of the reach stimuli. One possibility for this bias is because hand-related attention enhances functions on the behavioral level (Abrams et al., 2008; Fagioli et al., 2007; Reed et al., 2006; Schendel and Robertson, 2004) and on the neurophysiological level (Perry et al., 2015). Hand-related activity improves visual attention and alters visual processing (Perry et al., 2015). The alteration of visual processing could facilitate computing more specific details of an object for a potential usage by an upcoming function (Gutteling et al., 2011). The enhancement of perceptual sensitivity to the orientation was associated with grasping movement as opposed to pointing toward targets with different orientations (Abrams et al., 2008; Bekkering and Neggers, 2002; Gutteling et al., 2011; Hannus et al., 2005).

Our results indicate that for a given task, perception is focused toward those elements in the visual signals that would enable successful execution of the intended action. For instance, planning a grasping action enhances visual processing of relevant features, such as orientation. The perceptual system is “primed” toward these features

(Gutteling et al., 2011). The brain uses these features to enhance the accuracy of subsequent action, which is linked directly to the enhanced function at the perceptual level. That is, preparing a grasp action enhances the orientation perception of the target, and then the enhancement is used to improve the accuracy of the final grasp angle.

4.5. Grip Amplitude

Gaze and reach positions had no direct impacts on grip amplitude. However, our results showed that final grip amplitude was affected by the interaction of gaze and reach positions, and it was best explained in the eye-centred coordinate (target displacement relative to gaze). Our result is consistent with Selen and Medendorp's (2011) study, in which grip amplitude increased for objects at more eccentric locations relative to gaze, and these results suggest that grip aperture is represented in a gaze-centred reference frame. Larger amplitude for eccentric targets could occur as a result of the uncertainty (Selen and Medendorp, 2011).

Viewing targets from peripheral locations creates visual uncertainty of target location. When there is uncertainty in the system, estimates are degraded by each transformation made between coordinate frames. Grasping visual targets may compensate for uncertainty about object location (or size) by increasing grip amplitude (Schlicht and Schrater, 2007). Some studies found that maximum grip aperture was modulated by VFB (Sivak and MacKenzie, 1990; Wing et al., 1986). These results do not conflict with our results (as we found no VFB effects on the final aperture); maximum aperture reaches its peak during the movement, but it may be corrected for at the end of the movement and before contact is made.

4.6. General Discussion

Studies have shown that gaze-dependent errors were variable and depended on task conditions (Henriques and Crawford, 2000; Henriques et al., 1998; McGuire and Sabes, 2009). Previous studies tested gaze effects on single-point objects (except for Selen and Medendorp, 2011) while pointing towards (e.g., Henriques et al., 1998) or touching a target (McGuire and Sabes, 2009, Dessing et al., 2011) that is represented in a virtual environment. In these experiments, participants were asked to point at or touch using the right index finger. In our experiment, we used a slightly complex object that needed to be acted upon by a more complex action. The object's properties were used to dictate hand movement. The position of an object relative to gaze and the hand dictates transforming the hand toward the object's location, whereas an object's orientation and size dictate shaping the final grasp (angle and amplitude) appropriately.

By using more degrees of freedom in the task (small joints in the hand), we added another level of complexity to the motor system. Every time participants made a grasping movement, the object's properties and hand sensory inputs had to be computed relative to egocentric coordinates to produce a motor action requiring multiple joints coordination. In the early stages of visuomotor transformation, the brain encodes visual inputs in a gaze-centred coordinate. This information is used in the final stages of visuomotor transformation to control and guide hand movement in the body-centred coordinate (Selen and Medendorp, 2011; Andersen and Buneo, 2002).

In a grasping task, further transformation is required to estimate the final hand posture from the current hand posture. The biomechanical factors of the arm must be accounted for, and transformation from the kinematic to kinetics aspects of movement in body-centred coordinates is demonstrated during the visuomotor transformation process.

The processes of sensorimotor transformation are continuous and active. Accordingly, perception and action provide loops of feedback during the visuomotor transformation. This dynamic process and the redundancy of sensory modalities allow the brain to estimate an optimal mechanism that minimizes the errors associated with multimodal input integration. The optimization process weighs sensory signals depending on their relative precision and the task demand (Sober and Sabes, 2005; Ernst and Banks, 2002; Van beers, Sittig, and Gon, 1999).

Information about the object and hand arrives at different times through multiple sensory modalities, each by its own frame of reference. Maintaining an accurate representation requires both integrating and updating these sources of information after changes in the object's position and/or orientation, as well as changes in eye and hand direction. Moreover, accurate computation requires an accurate incorporation of the body geometry of the bones and muscles in the linkage from the eyeball to the hand (Henriques and Crawford, 2002).

Recent work by Sober and Sabes (2005) suggests that the brain selects coordinate representations that minimize errors caused by remapping. They give evidence that the strategy of selecting a frame of reference that is used to compute target location is flexible, and it selects to minimize errors, especially at the end of movement. They showed that altering the details of a task changes the relative weighting of visual and proprioceptive feedback used to plan the motor response. Sensory integration is not determined by sensory inputs but is influenced by the computations required for task execution. In addition, these changes occurred on a trial-to-trial basis as task conditions varied.

Our results are consistent with the idea that objects are processed differently depending on the task. During planning of a grasp, the brain utilizes essential information about the graspable object that is required to execute the movement (Ganel and Goodale, 2003). Our results may also reflect the differences in the neural circuits or patterns of activation that are engaged during the movement performance.

Neurophysiological and neuroimaging studies have showed that a gaze-centred frame of reference is used to represent and update target locations in specific areas in the PPC (Medendorp et al., 2005; Batista et al., 1999; Buneo et al., 2002; Snyder, 2000). The SPOC and the mIPS show eye-fixed sensory receptive fields and gaze position modulations suitable for transforming the hand to the target in visual space (Medendorp et al., 2003), whereas the PMd shows stronger hand and modest gaze modulations (Graziano and Gross, 1998; Cisek and Kalaska, 2002).

The lateral parietofrontal circuit (aIPS to PMv) shows activity related to grasp and grasp-relevant visual parameters (Muratta et al., 2000; Culham et al., 2003; Monaco et al., 2013). However, a recent study by Monaco et al. (2013) found that the SPOC and lateral occipital complex (LOC) process an object’s graspable dimensions during both grasping and viewing tasks. Both areas were involved in processing properties that were directly related to action stimulated by an object’s demands (Gibson 1979) even when the action was not planned. Their results are consistent with studies providing evidence for coding of intention in the dorsal stream (Snyder et al., 1997, 2000; Scherberger and

Andersen, 2007; Gallivan et al., 2011), and for coding action recognition in the ventral stream (Shmuelof and Zohary, 2005).

The PPC and occipital temporal cortex utilize grasp-relevant dimensions from an object's properties to use them for potential actions (Monaco et al., 2013, Culham et al., 2003; Cavina-Pratesi et al., 2007, 2010; Kroliczak et al., 2008; Gallivan et al., 2011). The aIPS also showed involvement in integrating information about graspable dimensions, such as an object's size (Monaco et al., 2013). Moreover, in animal studies, it has been found that the AIP was involved in modulating the intrinsic visual properties of objects (size). Some of the AIP neurons showed precise correspondence between preferred object and preferred grip (Murata et al., 2000).

The PMd is involved in the visuomotor representations of actions, in processing motor-related activity concerned with an object features, and in coding parameters of an object that are critical for grasp execution. Hand posture must be specified for the grasp-relevant dimension that is required by an object's features because different graspable objects require different postural adjustments of the digits and the hand. It is possible that the PMd is also involved in observing adaptation effects that reflect the sensorimotor feedback necessary for the control of grasping movements (Monaco et al., 2013).

The neural activity of M1 neurons was correlated to the extrinsic spatial kinematics of hand motion such as movement direction, distance, speed, and velocity (Moran and Schwartz 1999; Ashe and Georgopoulos, 1994). However, the neural activity in M1 neurons did not exclusively represent hand movement in either extrinsic or intrinsic coordinates. Neural modulation of the M1 was also correlated with the shoulder-centred coordinate (Wu and Hatsopoulos, 2006). Evidence has shown that the M1 is involved in transforming neural signals from an extrinsic-to-intrinsic coordinate.

The MI contributes to the internal model of limb mechanical properties that is necessary to resolve sensorimotor transformation and to compensate for the mechanical properties of the limb. Moreover, the M1 changes in a complex pattern, and its representation incorporates information about limb biomechanics provided by proprioceptive feedback (Sergio and Kalaska, 1997; Sergio and Kalaska, 2003; Sergio et al., 2005).

It is known that higher visual areas such as the occipito-temportal cortex are involved in processing global shapes (Felleman and Van Essen 1991; Van Essen et al., 1992; Maunsell and Newsome, 1987). However, studies have shown that early visual areas (V1, V2, V3, V4) are involved in the analysis of local features (Hubel and Wiesel, 1968) and in processing global visual configurations (Allman et al., 1985; Gilbert, 1992, 1998; Lamme et al., 1998; Fitzpatrick, 2000; Kourtzi et al., 2003; Kapadia et al., 1995, 1999; Zipser et al., 1996; Polat et al., 1998). In particular, V1 is involved in selective adaptation to global features in retinal periphery (Kourtzi et al., 2003) and object orientations (Poggio and Fischer 1977).

Physiological single-cell studies in V1 (De Valois et al., 1982; Mansfield, 1974; Poggio and Fischer, 1977) have reported that there are more cells tuned to horizontal and vertical than to oblique lines. However, other investigations failed to find significant differences in the numbers of cells tuned to different orientations outside the visual cortex (Campbell et al., 1968; Finlay et al., 1976; Henry et al., 1974; Hubel and Wiesel, 1968; Poggio et al., 1977; Rose and Blakemore, 1974; Wilson and Sherman, 1976). Several investigations have suggested that visual cortices are the site of origin for the oblique features of an object (Furmanski and Engel, 2000).

Smeets and Brenner (1999) have argued in favor of an alternative view. They suggested that reaching and grasping do not make up the movement; instead, grasping emerges from the trajectories of individual digits. Individual digits move independently to their respective sides of an object to be grasped. Thus, prehension is the combination of the movements of independent digits rather than the combination of reaching and grasping. In our experiment, we did not test for independent digit control. However, our general observation suggests a strong correlation between the positions of the two digits to form appropriate grip angle and size.

van de Kamp and Zaal (2007) assumed that if the thumb and index finger move independently to their respective end positions, altering the end position of one of the digits would not have an effect on the other. By comparing the kinematics of both digits, they found that changing the future end position of one of the digits had an effect on the same digit's kinematics and also on the kinematics of the opposing digit. Their finding conflicts with the idea of independent digit movements.

Some studies reported that pantomimed reaches use different neural circuits than natural reaches (Goodale, Jakobson, and Keillor, 1994; Westwood, Chapman, and Roy, 2000). They suggested that pantomimed actions are mediated by the ventral stream and natural actions by the dorsal stream. However, considerable evidence has shown that spatial information about objects is coded in multiple frames of reference (Beurze et al., 2010; Byrne et al., 2010; McGuire and Sabes, 2009). In our task, we examined the effects of visual inputs on pantomimed grasp parameters. The results of this study, consistent with Selen and Medendorp’s (2011) results, showed a gaze-centred nature. These findings suggest the potential involvement of the dorsal stream for pantomimed actions.

CHAPTER FIVE

5. CONCLUSION

The overall aim of this project was to evaluate eye-hand coordination during reach-and-grasp movement to oriented stimuli. We incorporated spatial plane changes, visual feedback, spatial memory, and arbitrary rules use in order to evaluate the adaptability of the sensorimotor control system. We increased the level of visuomotor complexity by changing the object demands to stimulate a complex sensory and motor computational process. The rationale for our method was that by adding these elements, we would alter the neural resources required to complete the task. Our procedure allowed us to quantitatively measure subjects’ ability to integrate visual information into a motor act.

Our results show that the brain processes sensory information relative to subjects’ frames of reference, and combines gaze and reach to estimate target and hand positions to plan the movement. These estimates produce noise and errors in the process of the visuomotor transformation. The weighting of sensory inputs was dependent on computational demands. The brain shows flexibility in choosing the type of sensory integration to minimize errors arising from the transformation of sensory signals between coordinate frames. Depending on the task context and visual feedback condition, the brain utilizes the sensory information that is crucial to execute movement.

Finally, the method used in this study allowed us to investigate interactions between object location, gaze direction, reach, and grasp at the behavioral level. We used the data to interpret the level of interactions that could occur in the underlying control mechanisms. Participants' performance of our task provided an indication about the brain's flexibility to effectively plan, perform, and integrate visuomotor transformations to complete reach-and-grasp tasks with respect to stimulus type and surrounding circumstances. This method could be used to assess and treat patients with visuomotor disorders in rehabilitation and clinical contexts.

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