DISSOCIATION OF GAZE ANCHORING IN REAL AND PANTOMIME REACH-TO-GRASP

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Dedication

For Cam and my Family

Abstract

Prehension consists of two temporally integrated components, a reach and a grasp, each mediated by distinct neural networks. Under visual control, the reach transports the hand to the target while the grasp simultaneously shapes the hand for target purchase. When prehension is performed from memory, as occurs in pantomime, the kinematics of the movement are altered. It is posited that real actions are primarily mediated via the dorsal vision-for-action stream and that pantomime actions are mediated via the ventral vision-for-perception stream. The purpose of the present thesis was to examine components of prehension under conditions of altered cues by monitoring gaze-point and hand kinematics. Removal of cues lead to the dissociation of the reach and grasp such that when the extrinsic properties were present and remained unchanged a real reach was performed with a pantomime grasp. Thus, the reach and grasp, have separate flexible mechanisms by which they can be mediated.

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List of Abbreviations

AIP/ aIPS	Anterior intraparietal sulcus
CNS	Central nervous system
GA	Grasp aperture
IPL	Inferior parietal lobule
IPS	Intraparietal sulcus
JND	Just noticeable difference
LGN	Lateral geniculate nucleus
LIP	Lateral intraparietal sulcus
M1	Primary motor cortex
mIPS	Medial intraparietal sulcus
MPA	Maximum pre-grasp aperture
PF	Parietal area PF
PFG	Parietal area PFG
PG	Parietal area PG
PMd	Dorsal premotor cortex
PMv	Ventral premotor cortex
PNS	Peripheral nervous system
RGC	Retinal ganglion cells
SPL	Superior parietal lobule
S1	Primary somatosensory cortex
SPOC	Superior parieto-occipital cortex
V1	Primary visual cortex
V2	Secondary visual cotex
V3A	Visual area 3A
V6A	Visual area 6A

Chapter 1
Introduction

1.1 Introduction

The pioneering work of Mishkin and Ungerleider (1972) on the two cortical visual systems sparked a cascade of research which lead to the modern theory of brain organization we have today: the action-perception theory. Mishkin and colleagues were the first to propose that there were two pathways, a ventral occipitotemporal pathway specialized for target perception or the ‘what’ pathway and a dorsal occipitoparietal pathway specialized for spatial perception or the ‘where’ pathway (1982). This two stream hypothesis was later revised by Milner and Goodale (1992) to incorporate a system that was reliant on output requirements. This distinction lead to a fundamental alteration from the ‘where’ pathway proposed by Mishkin to the ‘how’ pathway which was specialized for the guidance of actions. The functional dichotomy governing visuomotor processes, the dorsal stream for action and the ventral stream for perception, is an influential model of neural processing widely accepted amongst the neuroscientific community.

This dichotomy has been applied to the neural process that mediate actions made to objects that are physically present, a real reach-to-grasp, and actions that are made to objects that are no longer present, a pantomime reach-to-grasp. Specifically, the action-perception theory proposes that a real reach-to-grasp action is mediated online via dorsal visuomotor pathways and that a pantomime reach-to-grasp action is mediated offline via ventral visuotemporal pathways.

Vision plays a large role within the execution of action and an extension of the dorsal visuomotor pathway is the dual visuomotor channel theory that purposes that visually guided actions, such as reaching to pick up everyday objects, are composite movements featuring two distinct acts: a reach and a grasp.

I will review convergent evidence for the separate visual processing streams as well as the dichotomy of the dorsal visuomotor channel from behavioral studies, case studies, and neuroimaging studies. My thesis will begin with a brief definition of pantomime followed by a description of our sensory systems as they pertain to the control and execution of real and pantomime actions before I introduce and evaluate the current theory.

1.2 Pantomime

The term pantomime has a rich history across a range of disciplines that are quite diverse in nature such as theatre, dance, and research which makes defining the term difficult (Żywiczyński et al. 2018). Pantomime in theatre and dance originates from Roman mime, in which performers express meaning through gestures that are accompanied by music (Hall & Wyles 2008). Typically, pantomime theatre is designed for family entertainment and based off well-known fairy tale or fable. Pantomime, as it relates to research has its own meaning and can be found in developmental studies (Bartak et al. 1975; Scharoun Benson et al. 2018), studies on aphasia (Goodglass & Kaplan 1963), studies of apraxia (Heilman et al. 1982) and studies on motor control (Goodale et al. 1994; Culham et al. 2003). Jackson (1893) understood pantomime as a simple action designed to execute a relevant motor sequence in the absence of its object for transitive actions.

Due to the widespread use of the term pantomime, it is of importance to define pantomime as it appears in the present thesis. In research involving reach-to-grasp tasks, pantomime has taken on many forms as in some instances to pantomime a reach-to-grasp action means to perform the movement beside the target object, in the absence of the target, or even without all relevant cues (Goodale et al. 1994; Westwood et al. 2000; Bingham et al. 2007; Króliczak et al. 2007; Kuntz & Whishaw 2016). For this thesis, as we were interested in the effect of contextual cues on the hand kinematics and nature of gaze anchoring, so pantomime is broadly defined as completing a reach-to-grasp action without haptic feedback from the target object to be grasped. With this definition, context such as the visual and/or haptic availability of the grasping surface, the target object, or both can then be manipulated.

1.3 Sensation and Perception

Our experience, or our perception of the world is a unique interpretation of the raw information sent to our brains from a diverse set of sensory systems such as vision, audition, taste, olfaction, touch, and many others. Each of these sensory systems are organized within a hierarchy that begin with sensory receptors. These sensory receptors in turn have receptive fields to which they respond. This information is then passed through a neural relay where it is transduced and the information is now encoded by action potentials that travel along peripheral nerves in the somatic nervous system until they enter the brain or spinal cord to form our percepts. It is the brain that converges the multiple sensory modalities into a coherent percept upon which we can interact. Therefore, sensation and perception are intimately related and though they play complimentary roles they are vastly different. Evidence in support that perception is different from sensation is classically demonstrated in perceptual illusions in which different people transform the same sensory stimuli into vastly different percepts. The alternating perception of the same image demonstrates that the same sensory stimuli are affected by context, our emotional state, and by our past experiences. For example, Figure 1.1, is an ambiguous image that has two alternating perceptions, a duck or a rabbit, which are heavily influenced by context. Brugger and Brugger (1993) asked children to name the animal depicted in the picture at two timepoints; once on Easter Sunday and then later that year on a Sunday in October. They found that the identity of the animal was heavily influenced by context: identified as a rabbit more frequently at Easter and a duck later that year.

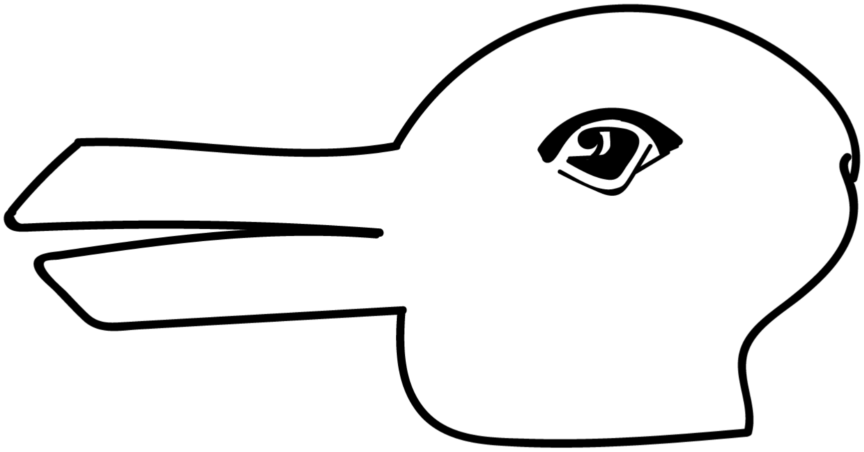


Figure 1.1 Rabbit-Duck illusion. Demonstration of the alternating precepts caused by the same sensory stimuli. This image is an adaptation of the original which first appeared on October 23, 1892 in an issue of Fliegende Blatter, a German humor magazine.

Our sensory system is frequently in action. For example, when we pick up an object to eat, multiple sensory systems are working together to process the task at hand, which in this case involves assessing several physical properties that make up the entity that we perceive as the target. If we say the target in this example is a blue skittle (a small candy), our visual system allows us to identify that the target is a skittle as our visual system assesses the size to be small and color to be blue. Our visual system also helps us locate where in space the skittle is, as well as its orientation which helps with initial planning of the movement. As the hand and arm move towards the target, proprioception and kinesthesia, the sense of knowing one's position in space, aids in directing the movement. Once contact with the skittle has occurred, hapsis, the sense of touch, allows for a bidirectional exchange of information i.e. the haptic contact made by the hand sends information to the brain about the size, shape, and texture of the target which allows for appropriate motor execution. Because my thesis primarily deals with the visual system and somatosensory system (hapsis-proprioception), these are the systems which I will briefly review.

1.4 Visual System

Our visual system provides us not only with detailed information of the world, but it also enables us to interact with our surroundings by guiding our actions. A large proportion of our brains are involved in visual processing: directly and indirectly. Vision begins at that level of the retina. Light energy stimulates the photoreceptors located on the retina and it is the photoreceptors along with the retinal neurons that transduce the light energy into action potentials (Schnapf & Baylor 1987). The retina contains two classes of photoreceptors which differ functionally and structurally: rods and cones. Rods are longer and have more cylindrical ends and are more numerous in comparison to cones. Further, rods are specialized to function in dim light making them advantageous for night vision whereas cones are highly responsive to bright light which enables them to mediate both our color vision and fine detail. The fovea, the central region of the retina, is specialized for fine detail and has an uneven representation of photoreceptors – only contains cones. Following stimulation of the photoreceptors, information is passed through one of three cell types (bipolar, horizontal, amacrine) to the retinal ganglion cells (RGCs) which form bundles that then leave the eye to form the optic nerve. RGCs consist of two types; magnocellular cells which are sensitive to movement and parvocellular cells which are sensitive to color and fine detail. The optic nerve from each eye partly cross before reaching the brain forming the optic chiasm. The optic chiasm results in half of each retina's visual field being represented on each side of the brain. There are then two main pathways to the visual cortex: the geniculostriate pathway and the tectopulvinar pathway (Schneider 1967). The geniculostriate pathway consists of both magnocellular and parvocellular cells whereas the tectopulvinar pathway, an evolutionary older system, consists of only magnocellular cells. These two pathways begin at the level of the retina but then differentialy transverse through the brain to visual cortical areas either in the parietal lobe or temporal lobe. Specifically, the geniculostraite pathway contains the lateral geniculate nucleus (LGN) the striate cortex while the tectopulvinar pathway contains the superior colliculus and the pulvinar and bypasses occipital visual areas.

The visual system also plays a role in perception of objects or object awareness. The posterior parietal lobule is subdivided by the intraparietal sulcus (IPS) into two main sectors: the superior parietal lobule (SPL) and the inferior parietal lobule (IPL). The latter includes areas parietal area PF (PF), parietal area PFG (PFG), parietal area PG (PG), anterior intraparietal sulcus (AIP), and lateral intraparietal sulcus (LIP) and is important for the processing of implicit knowledge (perceiving) visual stimuli. The most striking evidence for this reasoning is described by Marshall and Halligan (1988) in their series of experiments with a patient diagnosed with left-side visual neglect. When this patient was presented with two homes one above the other featuring identical right sides but different left sides (one was on fire). The patient did not identify any differences between the two homes, but when asked which house she would rather live in, she consistently selected the home that was not on fire. This result suggests that implicit knowledge of a stimuli can be processed without explicit awareness.

1.5 Somatosensory System

The somatosensory system is responsible for a wide range of sensations that are immediate, such as the pain experienced from a paper cut; as well as, sensations that go relatively unnoticed by our direct conscious experiences such as walking across the room or moving our arm through space to pick up an object.

It is the somatosensory system which conveys information to the spinal cord and the brain of our body. Unlike other sensory systems, such as the just discussed visual system, the somatosensory system is dispersed throughout the body and not localized to one area. Afferent sensory information is collected from receptors all over the body including body hair, skin, muscles, and tendons each of which has a different density which determines its sensitivity. For example, our hands have far more sensory receptors than our arms. Somatosensory receptors, though there are 20 or more, can be classified into three main groups: movement, pressure, and irritation (Lynn 1975) . Both pressure and movement are of utmost importance when executing reaching movements. Proprioception enables us to be aware of our body in space, and hapsis allows us to discriminate objects. In other words, when we reach out to grasp an object we know where our hand is in space because of stretch receptors in the muscles and tendons. Then once contact is made we can grasp an object appropriately using hapsis.

Haptic-proprioceptive information is carried to the CNS by the posterior spinothalamic tract. There are three relay neurons that send somatosensory information to the cortex: the posterior root ganglia neurons which respond to sensory receptor activation, the posterior column nuclei neurons which sends afferent information about the body senses, and the thalamic neurons receive the sensory information and sends them to the associated cortical area (Liang et al. 2011).

1.6 Motor System

The motor systems essentially allow us to react or to interact with our surroundings. These interactions can be of voluntary, such as reaching to pick up your morning coffee, or involuntary, such as blinking.

Penfield, over 50 years ago, used electrical stimulation of the human neocortex to confirm that movements are triggered by stimulation of the premotor and primary motor cortices. He found a motor homunculus, with disproportionate large facial features and hands in comparison to the rest of the body. Information represented in this motor homunculus (motor cortex) is primarily sent by efferent projections that transverse from the motor cortex to the brain stem and then the spinal cord via the corticospinal tracts or sometimes referred to as the pyramidal tracts. Most of the output axons originate in motor cortex layer V. These axons descend into the brain stem and at this point some of the axons from the right hemisphere cross over to the left, and vice versa for the axons from the left. The result is two corticospinal tracts entering the spinal cord: one crossed and the other uncrossed. The fibers that cross at the level of the brain stem form the lateral corticospinal tract and the fibers that remain on the ipsilateral side form the anterior corticospinal tract. At the level of the spinal cord, the fibers from either corticospinal tract make synaptic connections with interneurons and motor neurons. It is the motor neurons, however that communicate with the muscles to carry out nervous system commands. The lateral motor neurons project to muscles that control the hands, intermediate motor neurons project to muscles that control the shoulders and arms, and the medial motor neurons project to muscles that control the trunk. It is the lateral corticospinal tract that connects to the lateral and intermediate motor neurons. Hence the act of reaching is primarily produced by the lateral corticospinal tract. At the level of the muscle, communication occurs not only from the brain via the spinal cord motor neurons but also occurs through more immediate connections that coordinate simultaneous contraction and relaxation of muscle pairs (York 1987; Jang 2011).

1.7 Integration of Sensory and Motor Systems

Visual motor integration allows us to simultaneously use our hand and eyes to execute movements such as reaching to grasp targets, drawing, and catching.

Although it is the duty of the motor system to produce the movement, sensation directs the movement and gives the movement purpose. Therefore, the integration of multiple sensory systems is essential for successful movements. Afferent, or incoming, somatosensory information travels from the affected sensory nerve via the somatic nervous system. By way of a parallel network, the efferent motor system sends motor information, via the CNS, to produce movement (Kolb et al. 2016). Specifically, the primary somatosensory (S1) cortex is a major source of somatosensory input to the motor cortex (Jones et al. 1978). When this input is interrupted by selectively inactivating S1 with an agonist of GABA, manipulatory actions of the hand are lost (Hikosaka et al. 1985).

1.8 Action-Perception Theory

The Action Perception theory posits that that a real reach-to-grasp action or one that is ‘visually guided’ is executed online via the dorsal stream visuomotor pathways and a pantomime reach-to-grasp action or a reach completed to a remembered target is executed offline via the ventral stream visuotemporal pathways (Figure 1.2)(Milner & Goodale 2008).

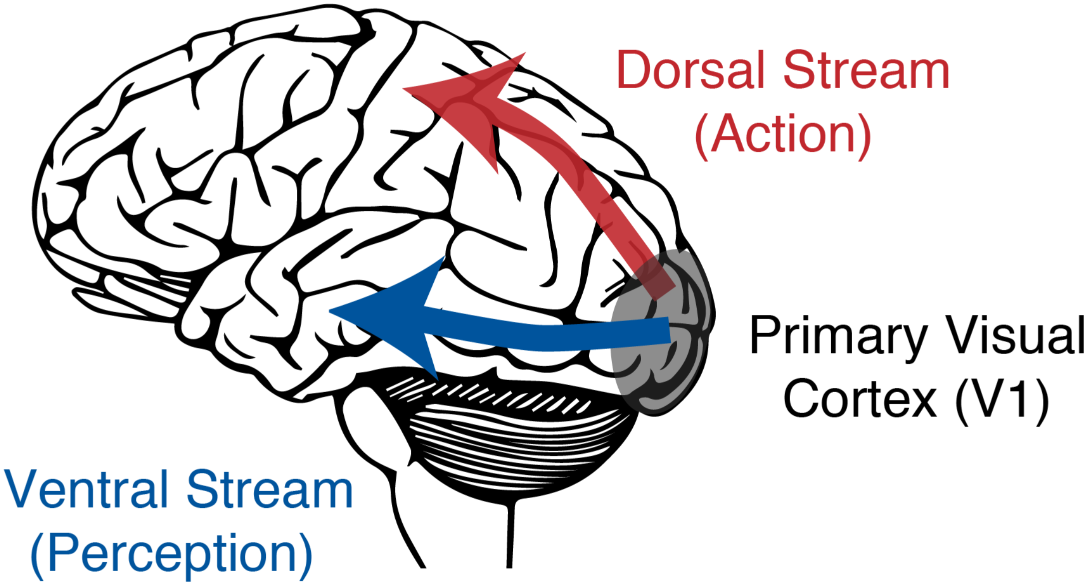


Figure 1.2 The action-perception theory. Dorsal visuomotor ‘action’ stream (red) and the ventral visuotemporal ‘perception’ stream (blue) originating from a common source within the primary visual cortex.

1.8.1 History

The action-perception theory in its current form is credited to work completed by Milner and Goodale (1995) and Goodale and Milner (1992); however, the theory's developmental history has an extensive past both in human and animal models. Trevarthen (1962) while working with split-brain monkeys proposed that there was a distinction between what he referred to as vision of relationships in space and vision for identification of objects. Similarly, Schneider (1969) proposed that in the golden hamster there was a dissociation between two visual systems: the geniculostriate pathway which mediated object identification and the tectal visual pathway which mediated orienting behavior. In 1973, Ingle also described two independent visual systems in frogs. But ultimately the work preceding that of the current model was completed by Ungerleinder and Miskin in 1982. In their study they serially disconnected parieto-preoccipital from striate cortex in monkeys and then tested them on a landmark task and a pattern discrimination task. Their work suggested that the differences in organization of striate inputs reflected differences in the processing of spatial and object vision. The primary difference between the theories preceding the current action-perception model of the organization of the visual system is that former models were based on a problematic distinction between 'what' and 'where' pathways while the latter is based on functional relevance of visions role in behavior. The action-perception theory receives support from psychophysical and neuropsychological studies. The section following will elaborate on each of these.

1.8.2 Psychophysical Evidence

Psychophysical evidence for the dissociations between action and perception, in large comes from studies using visual illusions. One such illusion is the Ebbinghaise-Titchener illusion in which two equivalent target circles are each surrounded by a circular array of either smaller or larger circles. When compared side-by-side, participants typically identify the target circle as larger when surrounded by the array of smaller circles than for the target circle surrounded by larger circles. Aglioti et al. (1995) used a modified three-dimensional version of this illusion whereby the middle targets could be grasped and discovered that the illusion remained effective on affecting perception. Calibration of the hand to the target, however was impervious to the effects of the illusory percepts and accurately scaled to the true size of the target, not the illusory one.

In summary, these studies show that although size-contrast illusions effect perceptual judgements of size, digit scaling remains accurate and therefore is not as susceptible to the visual effects of the illusion.

Psychophysical support for the action-perception theory also stems from work based on Weber’s law. Weber’s law, a fundamental principle of quantifying the perception of change for a given stimulus, states that the change in a stimulus that will be just noticeable is a constant ratio of the original stimulus; i.e., the just noticeable difference (JND) for a larger object should be larger than the JND for a smaller object (Laming 2008). A study completed by Ganel et al. (2008) tested the validity of Weber's law for visually guided actions by having participants make perceptual size estimates or grasp real objects of varying sizes. They discovered that physically grasping an object did not conform to Weber's law which contrasted with the perceptual estimates that did.

These studies are evidence in support that the different representations of the object utilized for action and perception are sustained by different neural controls.

1.8.3 Neuropsychological Evidence

Neuropsychological evidence, specifically that obtained from visual agnostic patient D.F., was critical in the foundation of the action-perception theory; so much so, that work continues to be published on her more than two decades after the first report. Patient D.F. sustained damage predominantly to the ventral stream with some bilateral posterior parietal damage (James et al. 2003; Bridge et al. 2013), following carbon monoxide intoxication. This irreversible damage rendered her incapable of perceiving the shape or orientation of an object but left intact her ability to use this information accurately during visuomotor tasks (Goodale et al. 1991). For example, when D.F. performed a task which required her to match a card to the orientation of a large, was required to physically turn a handle until it matched that of a slot, or was required to provide a verbal indication of the orientation of a block placed in front of her, her responses were variable and below chance. If she instead needed to physically place a card into the slot or grasp a block at multiple orientations, her accuracy was impeccable. Moreover, during both tasks correct orientation of the hand and/or card occurred early in the movement.

In sharp contrast to the performance of visual agnostic patient D.F. on tasks of perception vs action is optic ataxia patient I.G. For instance, when I.G. had to make a manual size estimate using the pointer finger and thumb to depict the size of the object displayed or when she had to pantomime a reach-to-grasp movement after a delay to a remembered target, she reliably shaped her hand to an appropriate aperture for the target (Milner et al. 2001). When required to reach out and grasp a target after a delay, performance broke down and digit scaling was highly variable. Therefore, patient I.G was capable of perceiving the correct orientation and shape of objects but was unable to accurately perform visuomotor actions as a consequence of bilateral damage to the posterior parietal area (Milner et al. 2001).

These patients demonstrate a double dissociation between the ability to complete a visually guided action towards a target and the ability to perform the same action to a removed target and thus support the idea that vision for action and vision for perception are mediated by different networks.

Behavioral studies of neurologically intact participants also suggest that real actions and pantomimed actions are mediated by different neural systems. For example, the behavioral kinematics of a real reach-to-grasp action are different from the kinematics of the same action pantomimed – whether it be pantomiming a reach-to-grasp in a location beside the target, pantomiming a reach-to-grasp action to a remembered target, or even pantomiming a reach-to-grasp action to a remembered target and location (Hu et al. 1999; Westwood et al. 2000; Kuntz & Whishaw 2016). These studies report that pantomimed actions take longer to complete, exhibit slower peak velocity, and have a smaller maximum pre-grasp and grasp aperture (Goodale et al. 1994; Westwood et al. 2000; Fukui & Inui 2013a; Holmes et al. 2013; Kuntz & Whishaw 2016; Kuntz et al. 2018).

1.9 Dual Visuomotor Channel Theory

The dual visuomotor channel theory purposes a functional segregation of the dorsal ‘action’ stream into the dorsodorsal pathway which mediates actions online and the ventrodorsal pathway which mediates motor control, comprehends action, and perceives space (Rizzolatti & Matelli 2003). In addition, the theory proposes that prehension consists of two components a reach and a grasp that occur concurrently under foveal vision but are each subserved by largely independent visuomotor pathways in the occipitofrontal (Figure 1.3). The dorsomedial Reach pathway projects through the superior parietal lobule via the parietal reach region, which includes the superior parieto-occipital cortex and the medial intraparietal sulcus. From here, it projects to the dorsal premotor cortex and then to primary motor cortex. The dorsolateral Grasp pathway transverses through the anterior intraparietal sulcus to the ventral premotor cortex and finally to primary motor cortex (Jeannerod et al. 1995; Rizzolatti & Matelli 2003; Culham & Valyear 2006; Cavina-Pratesi et al. 2010b; Filimon 2010; Davare et al. 2011)

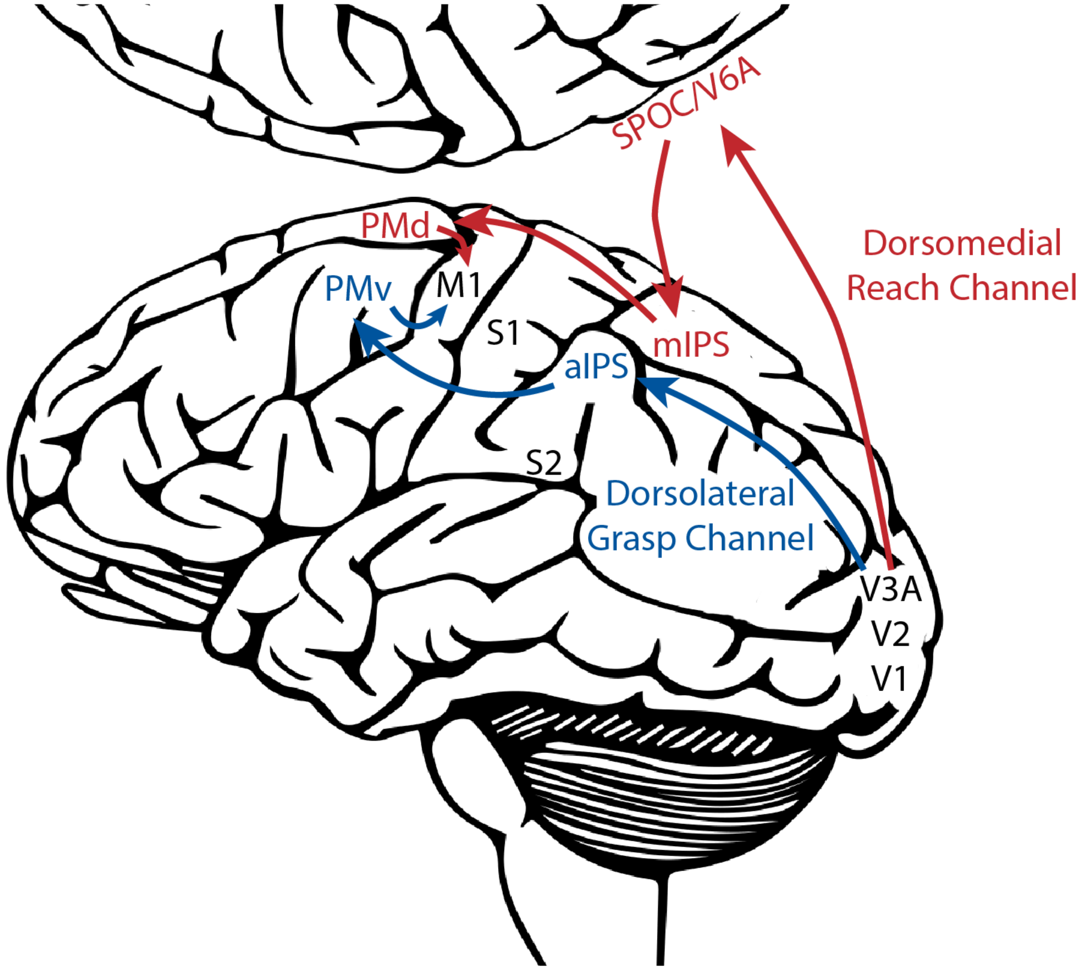


Figure 1.3 The dual visuomotor channel theory. The dorsolateral grasp channel (Blue) and the dorsomedial reach channel (Red), adapted from Grafton, 2010 (V1-Primary Visual Cortex, V2- Secondary Visual Cortex, V3A- Visual Area 3A, V6A -Visual Area 6A, aIPS- Anterior Intraparietal Sulcus, mIPS – Medial Intraparietal Sulcus, SPOC- Superior Parieto-Occipital Cortex, PMd -Dorsal Premotor Cortex, PMv- Ventral Premotor Cortex, M1- Primary Motor Cortex)

1.9.4 History

The dual visuomotor theory can be traced back to an observation that Woodworth (1899) made of the organization of a pointing movement. He proposed that pointing consists of two distinct phases; a ballistic movement positions the forelimb at the general target location, which is followed by a visually guided corrective movement made by the hand to make appropriate contact with the target. In 1981, Jeannerod proposed, based on the observations of patients with brain injury, that prehension too consisted of two distinct but temporally integrated movements: a reach and a grasp. The reach encodes information regarding the targets extrinsic properties, such as spatial location and is largely a proximal movement; whereas, the grasp involves more distal movements that shape the hand and digits in relation to the intrinsic properties of the target i.e. size and shape. These differences are summarized in Table 1.1. This theory has received support from behavioral, neuropsychological, and developmental studies.

Table 1.1 Characteristics of the Reach and Grasp Components

	Reach	**Grasp**
Musculature	Proximal	Distal
Function	Transport	Shape
Spatial Properties	Extrinsic	Intrinsic
Cortical Regions	Dorsomedial Parietofrontal Cortex	Dorsolateral Parietofrontal Cortex

1.9.5 Neuropsychological Evidence

Evidence in support of the distinct reach and grasp components of prehension comes from several human and non-human primate studies. Lesion studies have created a double dissociation from reach and grasp movements. Lesions localized to the caudal pole of the SPL and or the IPS produce impairments in visually guided reaching but not grasping (Cavina-Pratesi et al. 2010a). Patient M.H., who suffered an anoxic episode, has damage to the Reach but not Grasp pathways. He is capable of accurately shaping the hand and digits for target capture but only when the target is adjacent to his hand. When the target is moved, M.H. now has to execute a reach and he does this by first making contact with the target then grasping. On the other hand, lesions to the anterior intraparietal area in the anterior lateral bank of the intraparietal sulcus produce disturbances in grasping movements (Binkofski et al. 1998). Patients with this damage to the visual inputs to the grasp pathway reach to the targets location and make contact without issue this, however, the movement is changed and is now accomplished with an open hand (Jeannerod et al. 1994; Binkofski et al. 1998). In primate studies, long-train intracortical microstimulation of the distinct pathways mediating the Reach and Grasp components elicit independent reaching movements or independent grasping/manipulatory movements (Graziano et al. 2005; Gharbawie et al. 2011; Kaas et al. 2013)

Behavioral studies have long attempted to separate the reach and grasp by focusing on manipulating the target's properties. Jeannerod (1981) altered the extrinsic and intrinsic properties by altering the distance to the target and the target size and found that hand shaping and orientation were affected. Moreover, behavioral work where participants were required to reach out and grasp random food targets while blindfolded dissociated the reach from the grasp (Karl et al. 2013), such that the reach was used to first located the target without hand-shaping and then after contact with the target was established, haptic feedback guided the grasp. Behavioral attempts prior to this experiment failed to produce isolated change in either the reach or grasp components as modifications to either target location or size, introduced compensatory changes for the reach and the grasp (Jakobson & Goodale 1991; Paulignan et al. 1991; Paulignan et al. 1997).

The development of the seamless reach-to-grasp action occurs by combining the independent reach and grasp actions. At birth, infants possess the ability to orient their eyes and head to a visual target of interest; with pre-reach movements beginning shortly thereafter (Greenman 1963; Kremenitzer et al. 1979; VonHofsten & Rosander 1997). Infants early reach-like movements are made by the mouth by thrusting the head towards a target (Foroud & Whishaw 2012), followed by swiping haphazardly with an open or closed hand (Von Hofsten 1982, 1984) and using the forelimb to generate self-touching behavior

(Thomas et al. 2014). Pre-grasp movements are comprised of several small movements: closing the hand around a target that contacts the hand (Twitchell 1965), performing hand and grip configurations ‘hand babbling’ (Wallace & Whishaw 2003), and manipulating targets (Lobo et al. 2014). By 5 months of age, infants randomly begin to reach and grasp items under visual control, eventually developing the ability to both reach and grasp with a single integrated action (Sacrey et al. 2012b).

There is also argument in favor of independent evolutionary origins for the Reach and Grasp, which further strengthens the DVC theory. The reach is proposed to have its evolutionary origin based from limb stepping, whereas the grasp evolved from food handling behaviors (Karl & Whishaw 2013). In animals, a stepping movement is achieved by flexing the forelimb to release contact freeing up the limb to extend and establish another contact point (Grillner 1975). The forelimb has several uses besides its primary role in locomotion; i.e., independent forelimb use is seen for posture adjustment, digging, and fighting. Behavioral analyses of the structure of forelimb movements across several species for various behaviors lend support to the common origin for forelimb stepping and the reach. For instance, the series of movements that involve proximal movement of the forelimb, digit collection, and pronation of the hand for target capture or placement occur in walking in rats, crawling in humans, and for reaching for items.

Rationale for Thesis

Vision has a preeminent role during the reach and grasp movement. It is posited that concurrent visual inputs to the dorsomedial and dorsolateral pathways allow the simultaneous execution of the Reach and Grasp movement. Further, gaze anchoring, the act by which the target is foveated from movement onset until about the time of the grasp, is a characteristic feature of real reaching. What is unclear however, is whether or not the phenomenon of gaze anchoring is also a characteristic of pantomime reach-to-grasp movements. The purpose of the present thesis was to describe gaze point changes throughout the reach-to-grasp movement under conditions of altered contextual cues to determine visions contribution in shaping pantomime movements.

Theory

The action-perception theory posits that vision-for-action and vision-for-perception are mediated by distinct neural pathways, the former by dorsal stream pathways and the latter by ventral stream pathways. The dorsal ‘action’ stream transverses from early visual areas to the posterior parietal cortex, providing flexible control of online motor actions. The ventral ‘perceptual’ stream, on the other hand, transverses from early visual areas to the temporal lobe, providing detailed information required for identification. The reach-to-grasp movement, though temporally integrated under online foveal control, consists of two distinct movements: a reach and a grasp. According to the dual visuomotor channel theory of reaching the dorsal ‘action’ stream pathway that mediates motor actions has independent neural networks for mediating the reach and grasp components. The reach serves to transport and orient the hand in relation to the target’s extrinsic properties (location and orientation), while the grasp serves to shape the hand in relation to the target’s intrinsic properties (size and shape).

While both theories have received significant support from behavioral (Westwood et al. 2000; Karl et al. 2013), lesion (Goodale et al. 1994; Cavina-Pratesi et al. 2010a), and neuroimaging studies (Cavina-Pratesi et al. 2010b; Cavina-Pratesi et al. 2018). To our knowledge no investigation has directly tested the role of vision during pantomime when the context of the task has been visually and/or physically altered. Gaze anchoring assists both the reach and grasp during online actions. Specifically, gaze anchoring guides the reach to the correct location in space while allowing for online shaping of the digits (pre-shaping) to the targets shape and size prior to contact. Moreover, gaze anchoring is an essential feature for temporally integrating the reach and grasp components into the seamless act of prehension, without which we see a complete dissociation. If the properties such as the location and/or target are altered, as occurs in pantomime, we predict that vision will be altered from that used to guide a real reach-to-grasp.

Hypotheses

Hypothesis 1. If real and pantomimed reach-to-grasp actions are mediated by distinct neural pathways, as proposed by the action-perception theory, then these two actions may also be under different sensory control, specifically, the real reach-to-grasp action may differentially rely on visual attention compared to a pantomime reach-to-grasp action. Thus, I hypothesize that gaze anchoring, an indicator of attention, will be present for real but not for pantomime reach-to-grasp actions (Experiment 1).

Hypothesis 2. According to the dual visuomotor channel theory, prehension under visual control consists of two temporally integrated movements, a Reach and a Grasp. When context is altered during pantomime reach-to-grasp, the intrinsic and/or the extrinsic properties for the task have been changed. Thus, I hypothesize that gaze anchoring will vary as a function of the contextual cues of the task. (Experiment 2).

Experiments

Experiment 1. *Gaze Anchoring Guides Real but not Pantomime Reach-to-Grasp: Support for the Action-Perception Theory.* This experiment examined the differences in hand shaping and visual attention during a Real reach-to-grasp movement and a Pantomime reach-to-grasp movement for three target sizes. The Real reach-to-grasp task had participants reach out to grasp the target located on the pedestal directly in front of them; whereas, the Pantomime reach-to-grasp task had them pantomime this same movement in the absence of both the target and pedestal. The results suggest that (1) kinematics for the Real reach-to-grasp were coupled to the location and size of the target, but not to the same degree for the Pantomime reach-to-grasp, (2) gaze anchoring was tightly coupled to the targets for the Real reach-to-grasp task but no apparent organization of gaze was observed for the Pantomime reach-to-grasp task.

Experiment 2. *Contextual Cues Dissociate Reach and Grasp by Altering Gaze Anchoring for Pantomime: Further Support for the Dual Visuomotor Channel Theory of Reaching*. This experiment was designed to examine the effect of altered contextual cues on the kinematics and gaze of the reach-to-grasp action. Three pantomimed reach-to-grasp tasks (with varied contextual cues) and a Real reach-to-grasp to either a skittle or a donut ball were examined for differences in hand shaping and visual attention. The results suggest that (1) kinematics and gaze are affected by target size and task, (2) Decrease in contextual cues is concurrent with an increase in kinematic and gaze inaccuracy.

Chapter 2

Gaze Anchoring Guides Real but not Pantomime Reach-to-Grasp: Support for the Action-Perception Theory.

2.1 Abstract

Reach-to-grasp movements feature the integration of a reach directed by the extrinsic (location) features of a target and a grasp directed by the intrinsic (size, shape) features of a target. The action/perception theory suggests that integration and scaling of a reach-to-grasp movement, including its trajectory and the concurrent digit shaping, are features that depend upon online action pathways of the dorsal visuomotor stream. Scaling is much less accurate for a pantomime reach-to-grasp movement, a pretend reach with the target object absent. Thus, the action/perception theory proposes that pantomime movement is mediated by perceptual pathways of the ventral visuomotor stream. A distinguishing visual feature of a real reach-to-grasp movement is gaze anchoring, in which a participant visually fixates the target throughout the reach and disengages, often by blinking or looking away/averting the head, at about the time that the target is grasped. The present study examined whether gaze anchoring is associated with pantomime reaching. The eye and hand movements of participants were recorded as they reached for a ball of one of three sizes, located on a pedestal at arms-length, or pantomimed the same reach with the ball and pedestal absent. The kinematic measures for real reach-to-grasp movements were coupled to the location and size of the target whereas the kinematic measures for pantomime reach-to-grasp, although grossly reflecting target features, were significantly altered. Gaze anchoring was also

tightly coupled to the target for real reach-to-grasp movements but there was no systematic focus for gaze, either in relation to the virtual target, the previous location of the target, or the participant’s reaching hand, for pantomime reach-to-grasp. The presence of gaze anchoring during real vs its absence in pantomime reach-to-grasp supports the action-perception theory that real, but not pantomime, reaches are on-line visuomotor actions and is discussed in relation to the neural control of real and pantomime reach-to-grasp movements.

2.2 Introduction

A real reach-to-grasp movement to a visual target is different from a pantomime or pretend reach-to-grasp in which the target is absent. A real reach-to-grasp movement features scaling of hand's trajectory and digit shape in relation to a target whereas scaling for a pantomime reach-to-grasp is inaccurate relative to the pantomimed target (Goodale et al. 1994; Westwood et al. 2000; Fukui & Inui 2013b; Holmes et al. 2013; Kuntz & Whishaw 2016). One interpretation of the kinematic differences is that they support the action-perception theory. The theory proposes that real reach-to-grasp movements are online actions mediated by dorsal stream visuomotor pathways whereas pantomime reaches are offline actions mediated by ventral stream visuotemporal pathways (Milner & Goodale 2008). The action-perception theory is further corroborated by studies with neurological patients with visual form agnosia (D.F.) and optic ataxia (I.G.). Patient D.F. sustained damage largely to the ventral stream with some bilateral posterior parietal damage (James et al. 2003; Bridge et al. 2013) which hindered her ability to pantomime reach movements but left intact her ability to grasp real objects (Goodale et al. 1991). In contrast, patient I.G.'s bilateral posterior parietal damage impaired the real reach-to-grasp movement to a real object more severely than the same movement to a remembered object (Milner et al. 2001). Although both behavioral and neurological studies support the action-perception theory's explanation of real and pantomimed movements, a number of lines of research suggest that both real and pantomime actions are perhaps more complex in the form that they take and in their neural substrates. For example, the presence/absence of contextual cues can influence pantomime movements (Gentilucci et al. 1996; Coats et al. 2008; De Stefani et al. 2014; Kuntz & Whishaw 2016) as can the presence/absence of haptic feedback associated with grasping a real object (Bingham et al. 2007; Chan & Heath 2017; Jazi & Heath 2017; Rinsma et al. 2017). With respect to identifying neural pathways, fMRI activation in the dorsal stream occurs for both real and pantomime reaching, but in different hemispheres (Króliczak et al. 2007; Cohen et al. 2009). In addition, Vry et al. (2015) suggest that pantomime movement is mediated by at least two pathways, a dorsoventral pathway that is involved in the representation of the virtual target and a more ventral temporofrontal pathway projecting through the extreme capsule that represents the pantomime action (see also, (Hoeren et al. 2014; Goldenberg 2017).

A central characteristic of the visual control of real reach-to-grasp that likely contributes to its performance as an online movement is gaze anchoring. At about the time that a reach is initiated, a target is visually fixated and fixation is maintained until about time that the target is grasped. Visual fixation is disengaged, often with a blink and/or head aversion (Prablanc et al. 1979; Neggers & Bekkering 2000; de Bruin et al. 2008; Sacrey & Whishaw 2012a). Similar gaze anchoring occurs when participants point to a target (Neggers &

Bekkering, 2000; Prablanc, Echallier, Jeannerod, & Komilis, 1979). Because real reaching features two movements, the reach that directs the hand to the target guided by the extrinsic (location) features of the target, and the grasp that shapes the hand guided by the intrinsic (size and shape) features of the target (Arbib 1981; Jeannerod 1981; Jeannerod et al. 1994), gaze anchoring may be required to integrate these two movements. In the absence of gaze anchoring, as occurs when participants reach without vision or reach into peripheral vision, the reach and grasp dissociate such that the reach is used to locate the target and the grasp is formed in response to touch cues obtained from the target (Karl et al. 2012; Hall et al. 2014). Similarly, as the contextual cues available during pantomime reaching are reduced, there is a systematic loss of the integration of reach/grasp movements (Kuntz & Whishaw 2016). These findings raise the question of the extent to which the absence of movement scaling featured in pantomime reaching is due to the absence of visual control of the movement provided by gaze anchoring.

The purpose of the present study was to investigate whether a distinguishing feature of real vs. pantomime reach-to-grasp movements is the presence vs. absence of gaze anchoring. For the real reach-to-grasp task, participants reached for three targets, small, medium, and large balls that were located on a pedestal in front of them. For the pantomime task, the target ball and pedestal were absent and participants were briefly shown a ball and instructed to pretend to reach for it. Participants wore scene-based eye-tracking goggles as well as electromagnetic sensors attached to the hand to monitor eye and hand movements. This arrangement documented where participants were looking as they completed both real reaches and pantomime reaches.

2.3 Materials and methods

Participants

Participants were 21 right-handed young adults (11 female, 10 male; mean age 19.95 ± 0.9 months) recruited from Thompson Rivers University introductory psychology classes and received class credit for their participation. Each participant gave informed consent, authorized use of photos or videos, were self-reported as having no history of neurological, sensory, or motor disorders as well as normal, or corrected-to-normal, visual acuity. The University of Lethbridge and Thompson Rivers University, Human Subject Research Ethics Committees approved the study.

Apparatus

Participants were seated in a brightly lit room with a self-standing height-adjustable pedestal placed in front of them. The pedestal was placed at a horizontal reach distance normalized to the participant's arm length (100 % of the length of the shoulder to the tip of the index finger with the elbow at 180°

flexion) and the height of the pedestal was adjusted to the participant's trunk height, with 100 % of height from floor to outstretched arm while seated with the arm-shoulder at 90° flexion (Whishaw et al. 2002). This experimental setup allowed participants to naturally reach with their right hand towards the pedestal to pick up the target object as three measures of reaching behavior were made:

(1). Video recording. Two high-speed video cameras recorded behaviour throughout the task. Filming was performed at 30 Hz and 1/1000 shutter speed with cameras placed to capture both frontal and lateral views.

(2). Hand kinematics. Thumb, index, and wrist movements were acquired on-line at 60 Hz using a trakSTAR® (Ascension Technology Corporation) system. The position of the digits and wrist were calculated from electromagnetic sensors placed on the participant's hand; two on the distal phalanges of the thumb and index finger, and one on the wrist on the anterior aspect of the ulnar styloid, with respect to the transmitter. The transmitter was fastened to the floor beneath the participant's right chair legs such that the transmitter and the hands start position were vertically aligned.

(3). Eye movement. Eye movement was recorded using a ViewPoint EyeTracker® (Arrington Research, Inc) a monocular scene-based eye-tracking device. Eye-tracking glasses were worn for the entirety of the experiment and collected data at a sampling rate of 30 Hz. A sixteen-point eye calibration was performed prior

to data collection and was adjusted if necessary during the experiment (when there was a significant drift between gaze-point and the target to be fixated).

Reach targets

Participants reached for three targets (spherical balls) each with a different size: small (Circumference = 15.5 cm Diameter = 4.9 cm Volume = 19.1cm^3), medium (Circumference = 20.5 cm Diameter = 6.5 cm Volume = 33.4 cm^3), and large (Circumference = 22.5 cm Diameter = 7.2 cm Volume = 40.3 cm^3). Balls, rather than other target objects, were selected because a reach directed toward a ball is not influenced by intrinsic properties other than its size. The sizes of the balls were chosen based on preliminary experiments in which participants reliably judged that the balls represented increasingly larger sizes. The small and medium targets had a rougher surface compared to the smoother plastic of the large target. The textual properties and surface colorations were intentionally chosen to be different so as to not distract the participants from the size differences. Targets were placed at the centroid of the pedestal prior to trial initiation.

2.4 Procedure

A participant was seated in a comfortable upright position with their feet flat on the floor with their hands placed in the start position. The start position for the right hand was marked on the dorsum of the upper thigh, and participants started with their thumb and index finger in opposition; whereas, the left hand was resting in an open and relaxed position on the dorsum of the left upper thigh. Participants were then presented with a set of practice trials where they reached out and grasped an object and brought it back to their chest. This was done so that participants would not only be accustomed to the task, but to ensure that the equipment would not interfere with their natural reach-to-grasp movement.

Participants adopted the start position between trials and waited for a start prompt which was a verbal “1-2-3- GO” command. The experiment consisted of two tasks;

(1). Real reach. For the real task, participants were instructed to “reach out and grasp the target and bring it back to your chest”.

(2). Pantomime reach. For the pantomime reach, a participant was shown a ball for which they should reach, but the ball was not present during the reach. The pedestal was also removed because preliminary work suggested that if it were present the task would in part comprise a pointing task for which gaze anchoring would be present (Neggers & Bekkering, 2000; Prablanc, Echallier, Jeannerod, & Komilis, 1979), a feature that would thus confound the objectives of the present study. The instructions for the real reach and the pantomime reach tasks were otherwise similar, the participants were instructed to “reach for

the real ball and bring it to your chest", or instructed to "reach out and grasp the (small, medium or large) ball at the same location as you had for the real condition and bring it to your chest."

All reaches for the real task were completed prior to the pantomime task. This was done to ensure that all participants were familiar the real task before they performed the pantomime.

Experimental Design

The study used a 2X3X3 repeated-measures within-subjects design. Each participant performed the reach-to-grasp movement under 2 task conditions (real vs. pantomime), for 3 different sized targets per task (small, medium, large), at a rate of 3 trials (1, 2, 3) per target per task. Trial number was based on previous reach-to-grasp studies (Karl et al 2013). This experimental design, allowed for adequate statistical power while ensuring participants remained attentive. Thus, each participant completed a total of 18 reaching trials. Each scenario is illustrated in Figure 2.1. Figure 2.1(A-C) illustrates the real reach task with a ball of each of the three different sizes, and Figure 2.1(D-F) illustrates the pantomime reach task.

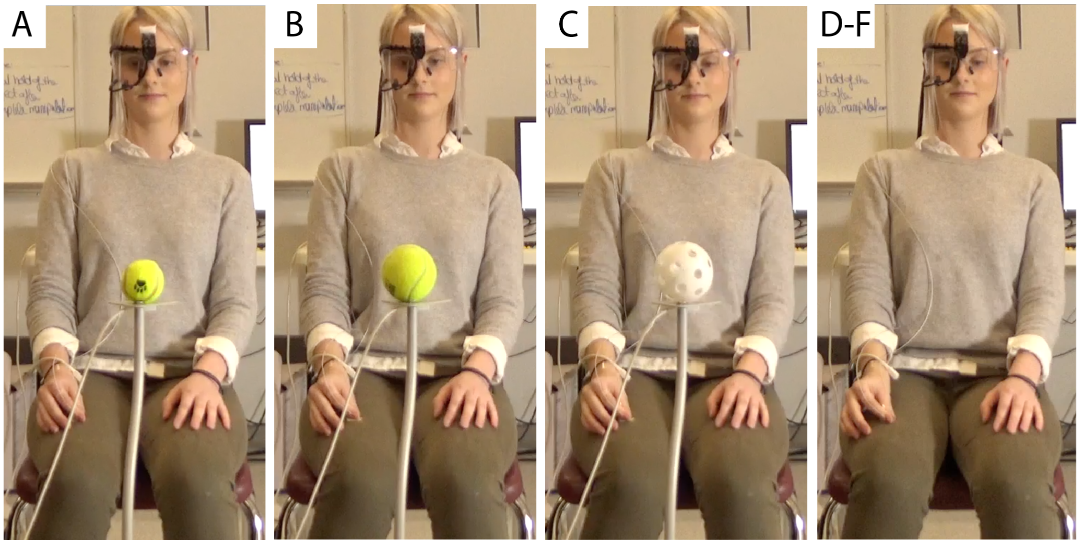


Figure 2.1 Real and pantomime conditions. A) *Real Small,* B) *Real Medium,* C) *Real Large.* In the real conditions participant reached from lap for a ball (small, medium, large) located on a pedestal at arm's length and brought the ball back to the chest. D-F) *Pantomime (Small*, *Medium*, *Large).* In the pantomime conditions neither the ball nor the pedestal were present.

2.5 Data Analysis

Hand Movements

Kinematic events were processed offline using custom-written algorithms created in Matlab® (Version R2016b; The Mathworks, Natick, MA, USA). A participant made a lateral movement with the reaching hand before they placed the hand in the start position with the first two digit in opposition. On the kinematic record, this movement was used to separate data into discrete trials. Movement initiation was defined as a minimum wrist velocity threshold of 5mm/sec in the frontal direction after the 1-2-3- GO command. Withdraw was defined as occurring after the grasp and constituted a backwards movement of the hand back to the body. The reach-to-grasp movement then consisted of measures between reach initiation to withdraw. Kinematic measures determined from the data consisted of the following:

(1). Maximum pre-grasp. Maximum pre-grasp was defined as the maximum index-thumb aperture obtained between the movement initiation and grasp.

(2). Grasp. Grasp was defined as the minimal closing aperture between the index finger and thumb, prior to the beginning of the withdraw movement.

(3). Maximum height. Maximum height was defined as the maximal vertical displacement of the index prior to the beginning of the withdraw

movement and was measured relative to the surface of the pedestal platform.

(4). Reach Duration. Reach duration was defined as the time difference between movement start and grasp.

Gaze Direction

Participant visual fixations, relative to the visual scene in front of them, were analyzed offline using Point Picker (ImageJ, Natick, MA, USA). In the real reach task, relative gaze measures were calculated from 8 points that were identified by stepping through the visual fixation data frame-by-frame. The 8 points were the tips of the thumb and index finger, the three corners of the pedestal, the fixation point, and the center of the target. For the pantomime reach tasks, 4 points were identified: tips of the thumb and index finger, the tripod block of the camera positioned in front of the participant, and the fixation point. Sometimes the eye-tracking was dropped due to frequent blinks, incompatible eye-shape and for other for unknown factors. If the eye tracking was lost at an abnormal rate on multiple trials across reach scenarios data from that participant was discarded; therefore, eye movement results are derived from 17 subjects. The locations of visual fixations were derived from these measures.

(1) Visual distance. Measures of visual fixation were taken at three different time points during each reaching trial: Movement initiation, Midpoint of hand transport– defined as 50% of reach duration, and Termination of reach signified by a grasp. Three measures of gaze fixation were taken at each time point:

i) Distance of gaze fixation relative to the center of the pedestal. The mean position of the center of the pedestal in the real condition was defined as the location of the "center of the pedestal" in the pantomime condition.

ii) Distance of gaze fixation relative to the midpoint between the thumb and index finger.

iii) Distance of gaze fixation relative to the eventual grasp location as indicated by the midpoint between the tip of the thumb and index at the time of grasp for that trial.

(2). Visual trajectory. To calculate the gaze trajectory associated with the real reach-to-grasp movement and the pantomime of the movement, the distance between gaze fixation and the center of the pedestal was measured on each frame, beginning 10 frames prior to reach initiation and ending 5 frames after grasp completion. Data were interpolated to plot average visual trajectory in relation to reach time.

Statistical Analysis

All data were analyzed using a repeated-measures, analysis of variance (RM-ANOVA) and ANOVAs of the coefficient of variation, when appropriate, using the statistical computer program SPSS (v.24.0.0). A p value of < 0.05 was considered significant.

Data for gaze fixation relative to the pedestal, gaze fixation relative to the hand, and gaze fixation relative to grasp location were analyzed using Time (Initiation, Midpoint, Grasp), Task (Real, Pantomime), Size (SM, MD, LG), and Trials (1, 2, 3), as the within-subjects factors. Visual Trajectory data was calculated by using Fixation Point (relative to Pedestal, relative to Hand), Task (Real, Pantomime), Size (SM, MD, LG), Trials (1,2,3), and Frame (1-30) as the within-subjects factors.

Hand movement data was calculated by using Task (Real, Pantomime), Size (SM, MD, LG), Trials (1,2,3), as the within-subjects factor for the separate dependent variables of Maximum Pre-Grasp, Grasp, Maximum Height, and Reach Duration. Additional tests of variance were calculated for kinematic data for Group (RealSM, RealMD, RealLG, PantSM, PantMD, PantLG). Post-hoc tests with Bonferroni corrections were completed after statistical significance was determined. Results are reported as mean ± standard error.

2.6 Results

Reach duration

Reach-to-grasp movements for both real and pantomime conditions were completed in under 0.8 seconds, but the time to complete a real reach was significantly longer than the time to complete a pantomime reach, $F(1,16) = 6.693$, $p = 0.020$. There was a significant main effect of ball size, Size $F(2,32) = 5.259$, $p = 0.011$, and post-hoc tests with Bonferroni correction indicated that the average duration was longer for the small ball than for the medium and large balls for both real and pantomime reaches ($p < 0.001$). There was no significant main effect of Trials, $F(2,32) = 0.397$, $p = 0.676$ nor a significant interaction of Task by Size $F(2,32) = 0.175$, $p = 0.840$.

Maximum pre-grasp aperture and grasp aperture

Figure 2.2 shows that both maximum pre-grasp aperture and grasp aperture, were larger for real reaches than for pantomime reaches, although both measures increased with ball size for both real reaches and pantomime reaches. The difference in maximum pre-grasp aperture between real reaches and pantomime reaches (Figure 2.2A) was not significant $F(1,20) = .041$, $p = 0.842$, but there was a significant main effect of ball size (Size $F(2,40) = 41.58$, $p < 0.001$). Further there was no significant interaction of Task by Size, $F(2,40) = 1.478$, $p = 0.240$. Nevertheless, the boxplots of maximum pre-grasp aperture size in Figure 2A did suggest that there was greater variance in the maximum pre-grasp aperture size for the pantomime reaches vs real reaches. This was confirmed by running an ANOVA of the coefficient of variation, $F(5,377) = 26.361$, $p < 0.001$. Follow up paired samples t-tests revealed significant differences in the scores for Real small (M= 0.1362 cm, SD = 0.1018) and Pantomime small (M= 0.1862 cm, SD = 0.1238) coefficient of variation; t(62)= -2.228 , p= 0.030, and Real large (M= 0.1041 cm, SD = 0.0664) and Pantomime large (M= 0.1375 cm, SD = 0.1015) coefficient of variation; t(62)= -2.055 cm , p= 0.044.

An ANOVA of grasp aperture (Figure 2.2B) showed that that grasp aperture size was larger for real reaches than for pantomime reaches, Task, $F(1,20) = 12.930$, $p = 0.002$. Further, the grasp aperture increased with target size as was confirmed by a significant main effect of Size $F(2,40) = 63.026$, $p < 0.001$. No significant interaction between Task by Size, $F(2,40) = 0.319$, $p = 0.729$ was found. Follow-up analyses indicated that the small, medium, and large ball sizes were all significantly different from one another in both tasks. In addition, the boxplots in Figure 2.2B suggested that there was greater variance in grasp aperture for pantomime reaches vs real reaches, which was confirmed by a significant coefficient of variation for Task $F(5,377) = 6.103$, $p < 0.001$.

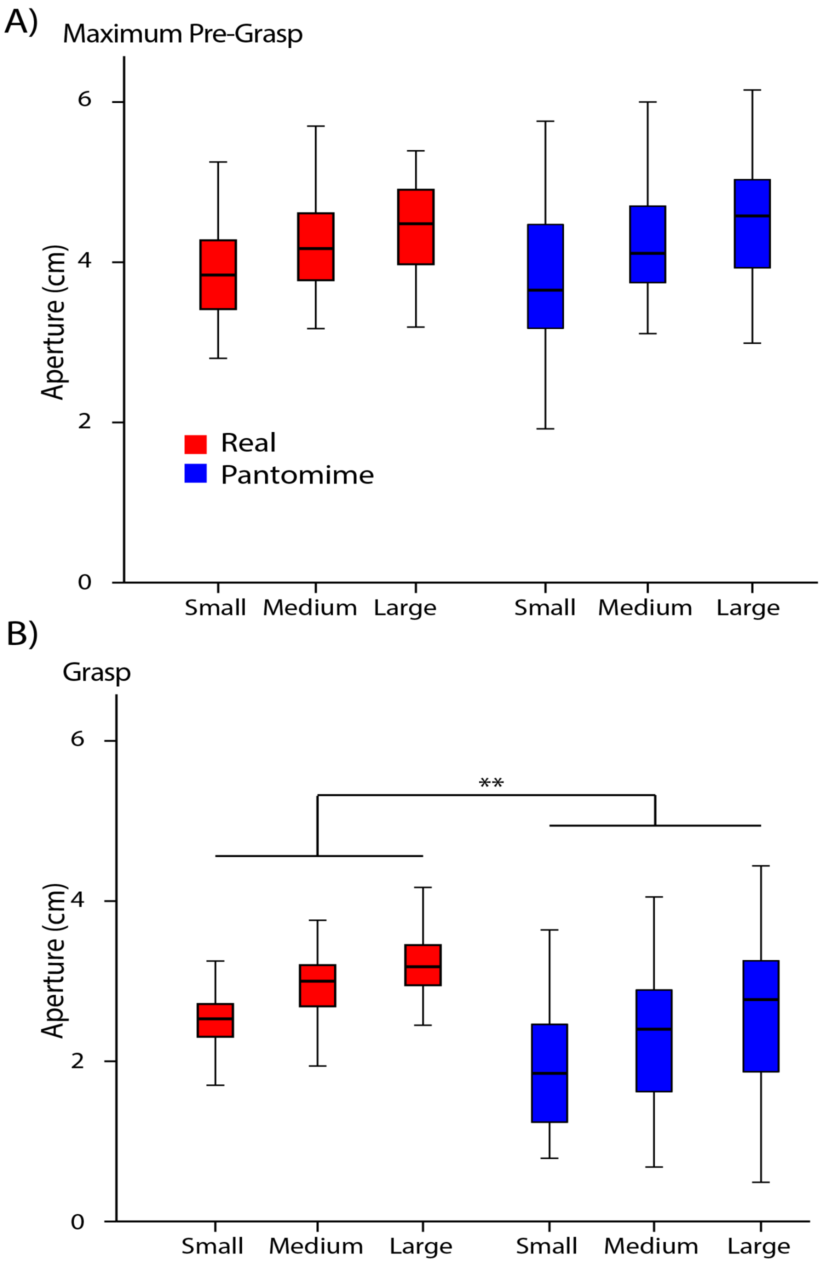


Figure 2.2. Maximum pre-grasp and grasp aperture. A. Box plot of aperture at maximum pre-grasp in Real (red) and Pantomime (blue) conditions showing the third quartile (Q3) and first quartile (Q1). B. Box plot of aperture at grasp in Real (red) and Pantomime (blue) conditions. (**$p < 0.01$). Note: aperture variability is high in Pantomime conditions.

Maximum reach height

Figure 2.3 summarizes the results of maximum height of the index finger relative to the surface of the pedestal for the real reach vs the pantomime reach tasks. Peak height increased with target size as was confirmed by a significant main effect of Size, *F*(2,40) = 21.485, $p < 0.001$. Post-hoc tests with Bonferroni correction revealed significant difference for the small and medium ($p < 0.001$) and the small and large target ($p < 0.001$), but not for the medium and large target ($p > 0.05$). An ANOVA also revealed a significant main effect of Task *F*(1,20) = 18.333, $p < 0.001$. Follow up Post-hoc tests with Bonferroni correction revealed significant differences in the peak height scores for Real small (M= 0.0344, SD = 0.0392) vs. Pantomime small (M= 0.0778, SD = 0.0689) coefficient of variation; t(62)= -5.842 , p= 0.000, Real medium (M= 0.0476, SD = 0.0611) vs. Pantomime medium (M= 0.0707, SD = 0.0076) coefficient of variation; t(62)= -2.940, p= 0.005, and Real large (M= 0.0281, SD = 0.0342) vs. Pantomime large (M= 0.0710, SD = 0.0081) coefficient of variation; t(62)= -4.884, $p < 0.001$.

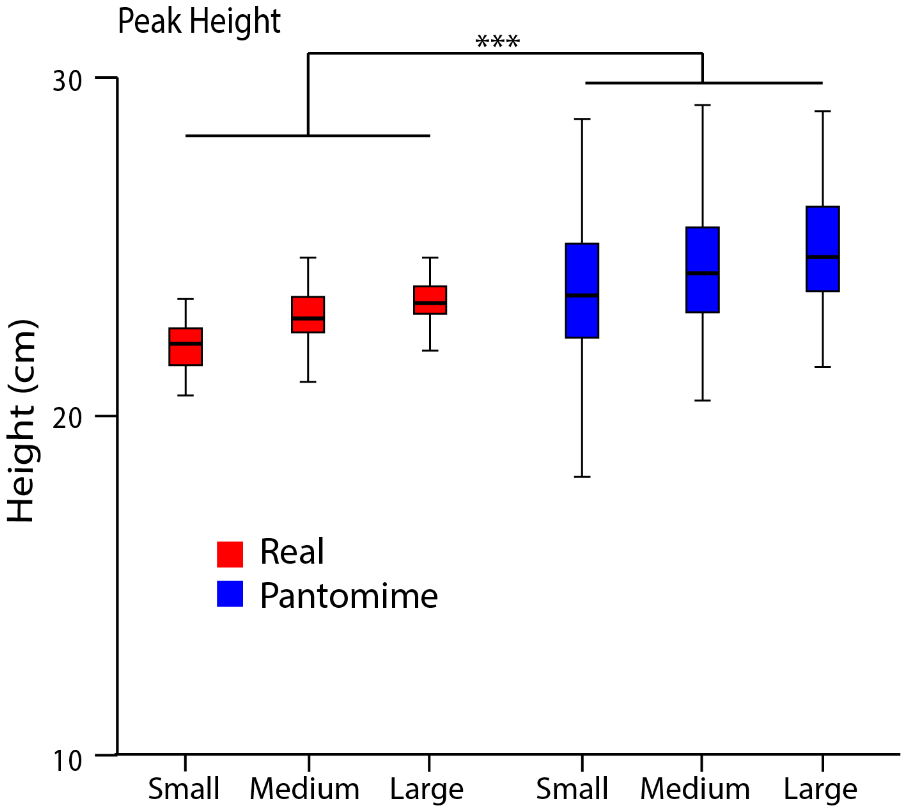


Figure 2.3. Box plot of maximum height of the index finger in Real (red, left) and Pantomime (blue, right) conditions showing the third quartile (Q3) and first quartile (Q1). (***p <0.001) *Note:* variability is greater in Pantomime conditions.

Gaze direction

The gaze direction of participants on the real reaching task was directed to the target from movement initiation to about the time the target was grasped. Figure 2.4-top shows a typical example of gaze anchoring, in which gaze remained on a target during a participant's real reach. During pantomime, there was no systematic relationship between gaze and the target and Figure 2.4-bottom shows an example in which gaze is directed well above the virtual target at initiation, approximately halfway through the reach, gaze is briefly directed towards the participant's hand and then quickly returns to a point above the target. Support for the differences for this general finding is given in the following paragraphs.

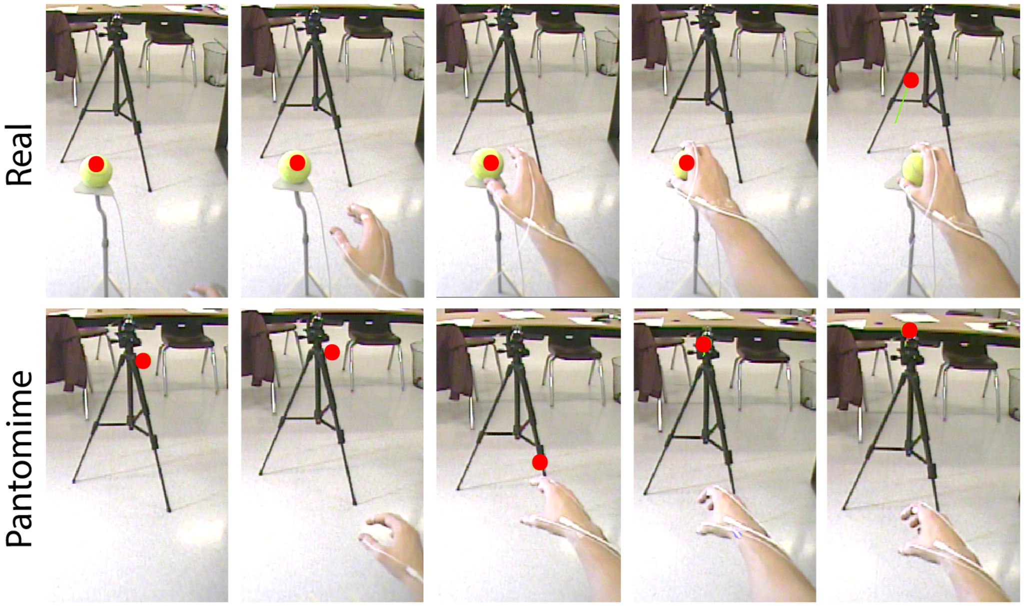


Figure 2.4. Still frames of gaze-point and reach behaviour taken prior to reach initiation until withdraw of the hand for the medium sized target in the Real condition (top) and Pantomime condition (bottom).

Figure 2.5 shows that the distance between visual fixation and the pedestal at reach initiation, reach midpoint, and grasp was smaller for the real reach task than the pantomime reach task. Figure 2.5-Left shows that gaze distance for the real reaches at reach initiation, the midpoint of the reach, and at the grasp was significantly closer to the platform than it was for pantomime reaches. That the gaze fixation point for real reaches was closer to the platform than that of pantomime reaches was confirmed by an ANOVA that gave a significant main effect of Task $F(1,16) = 33.249$, $p < 0.001$. There was a significant main effect of Size $F(2,32) = 5.768$ $p = 0.007$ but no significant main effect of Time $F(2,32) = 0.666$ $p = 0.521$.

Figure 2.5-Right shows gaze fixation position relative to the pedestal's surface for all ball sizes of each participant. The distance of the gaze fixation points relative to the center of the pedestal surface at reach initiation, reach midpoint, and grasp for individual participants was smaller for the real vs. the pantomime task. At all three time points in the real reach task, most participants fixated the target, as is represented by the dense population of red symbols above the pedestal. Only at reach initiation and grasp was there variation in gaze fixation in the real reach task (when participants initiated gaze anchoring or disengaged gaze anchoring). The fixation points for the pantomime reaches were more frequently displaced from the virtual platform location and

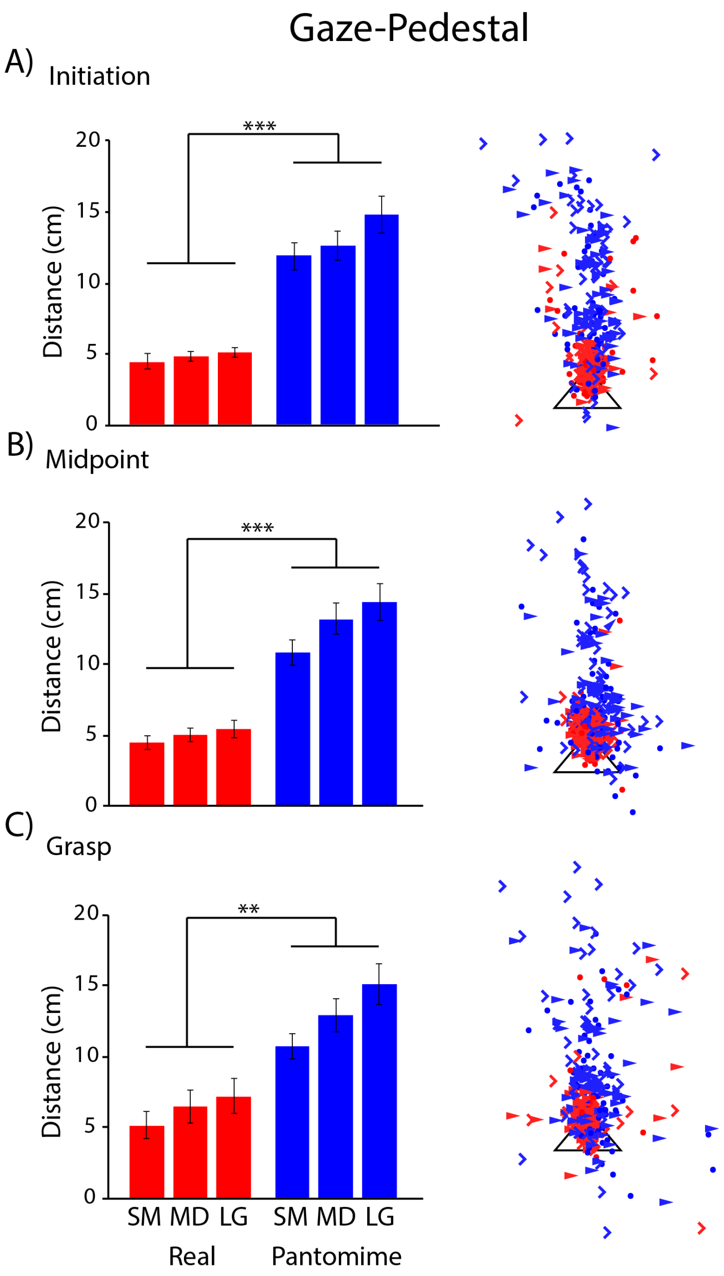


Figure 2.5. Visual fixation relative to the pedestal at three time points of the reach. Left. Average absolute distance from point-of-gaze to center of the pedestal (mean ± standard error) in the real (red, left) and pantomime (blue, right) condition at three time points: A) Initiation, B) Midpoint, and C) Grasp. (**$p<0.01$, ***$p<0.001$). Right. Visual fixation points of all participants relative to the pedestal. Average distance from point-of-gaze to the center of pedestal for the entire reach-to-grasp movement in the Real and Pantomime condition for three target sizes: Small •, Medium ▶, and Large ➤. *Note* visual trajectory is closely linked to the target's location for the Real reaches but is more variable for Pantomime reaches.

were more variable at all points in the reach as is indicated by the more dispersed blue symbols.

Figure 2.6 illustrates that the absolute distance between the gaze point and the center of the platform of the pedestal was maintained throughout the reach in the real reach task. That is, once the reach was initiated, gaze was directed to, and then anchored on, the target until the target was grasped in the real reach condition. There was no similar gaze anchoring for the pantomime reach task. An ANOVA on gaze location distance relative to the platform confirmed that real reaches were different, in that they were more closely anchored on the target, than pantomime reaches, Task, $F(1,16) = 32.090$, $p < 0.001$. There was also a significant main effect of frame of the reach with the gaze fixation point being directed to the target at the beginning of the reach and away from the target at the end of the reach, with maximum fixation on the target occurring around the midpoint of the reach, which was greater for real reaches vs pantomime reaches. This finding was confirmed by a significant main effect for Frame $F(29,464) = 5.249$, $p < 0.001$, and a significant interaction of Task x Frame $F(29,464) = 2.524$, $p < 0.001$. No significant interaction for Task x Size $F(2,32) = 0.998$, $p = 0.380$ was observed.

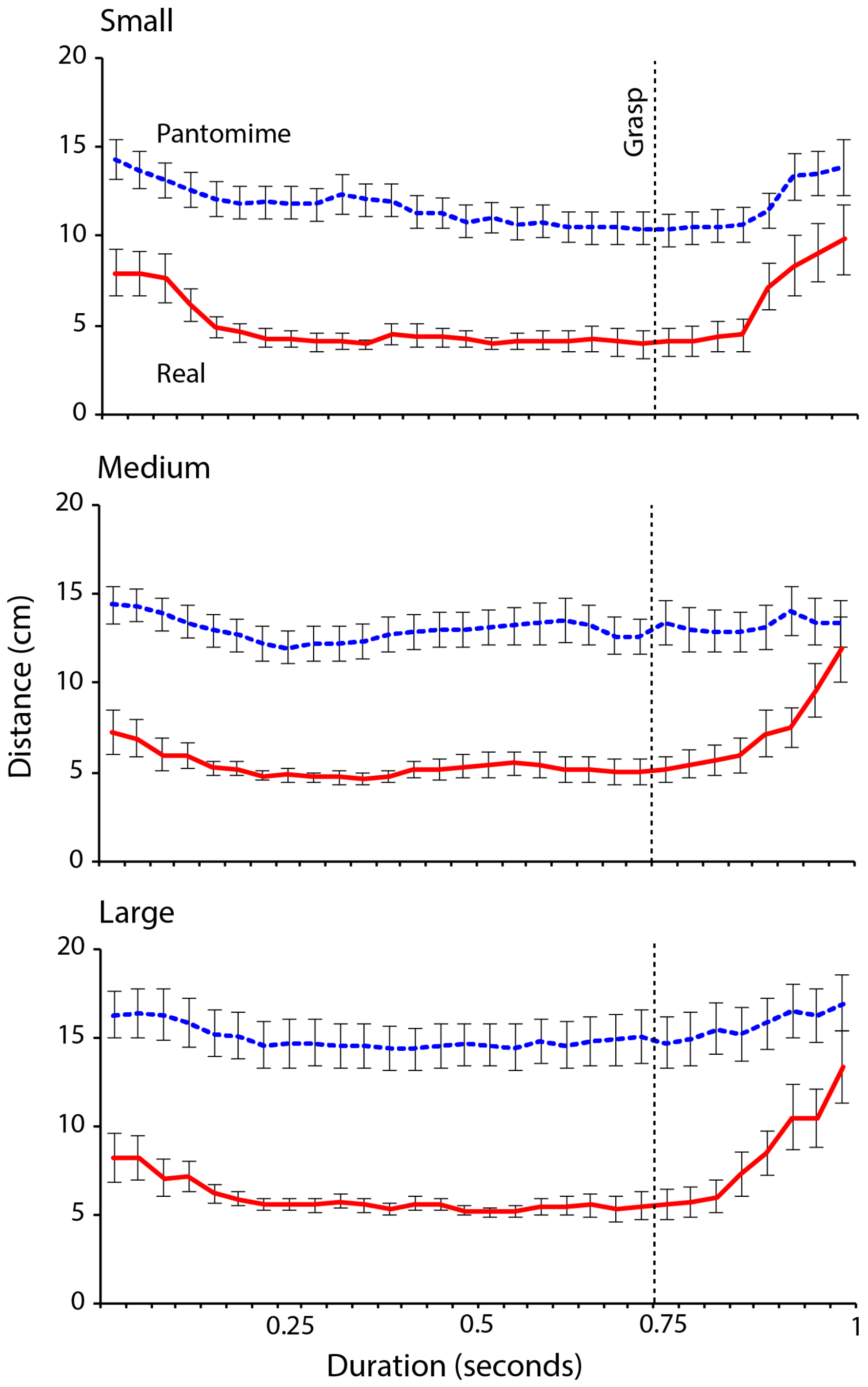


Figure 2.6. Visual fixation throughout the reach relative to the center of the platform for real (red) and pantomime (blue) reaches (mean ± standard error). *Note*: The gaze point is directed toward the pedestal at the beginning of the reach and away from the pedestal at the grasp for real reaches but not for pantomime reaches.

Additionally, Figure 2.7 shows that variance in gaze location relative to the pedestal surface decreased as a real reach was initiated specifically in the latter two thirds of the reach. Variance during the pantomime condition did not follow this trend and exhibited greater variance with minimal change with reach progression.

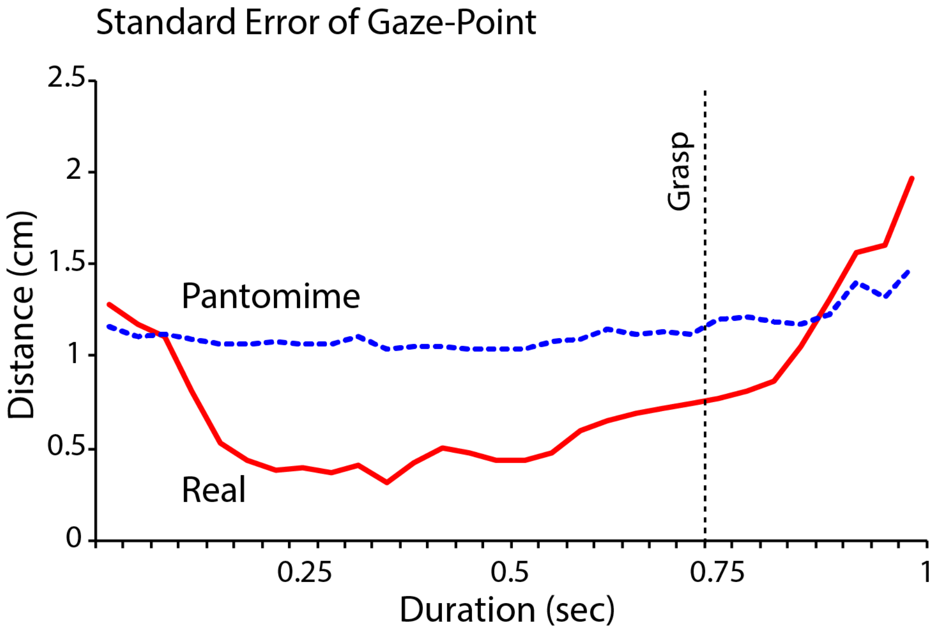


Figure 2.7. Average variance for all real and all pantomime reaches relative to the center of the platform on which the target is located (mean). *Note* the decrease in variance for real reaches is smallest shortly after the reach is initiated but there is little change in variance for pantomime reaches.

Distance of Gaze fixation point relative to the hand and virtual target

The finding that gaze is directed to the platform throughout the duration of the real reach task, raised the question of whether there was any systematic gaze direction for the pantomime reach task. There were two possibilities: participants in the pantomime task might be looking at their hand or they might be looking at the virtual target, i.e.; the location at which they will make a grasp movement.

Figure 2.8A shows that during the pantomime task, participants did not fixate on the reaching hand at any of the time points measured: initiation, midpoint, and grasp. Figure 2.8A shows that as the reaching hand approached the target, the distance between gaze fixation and the hand location for real reaches decreased (because the hand was approaching the gaze fixation point near the pedestal). These differences between the real and the pantomime task were confirmed by an ANOVA that gave significant main effects of Task, $F(1,16) =35.220$, $p < 0.001$, Time, $F(2,32) =210.730$ $p < 0.001$, and a non-significant interaction of Time x Task, $F(2,32) =0.005$, $p = 0.995$. For pantomime reaches there was only a slight tendency for participants to direct their gaze toward the reaching hand and then only for the terminal point of the reach and mainly for smaller ball sizes, but this did not reach statistical significance. The ANOVA also gave a significant main effect of ball size, Size, $F(2,32) =11.665$, $p < 0.001$ and an interaction between task and ball size, Task x Size $F(2,32) = 5.698$, $p = 0.008$.

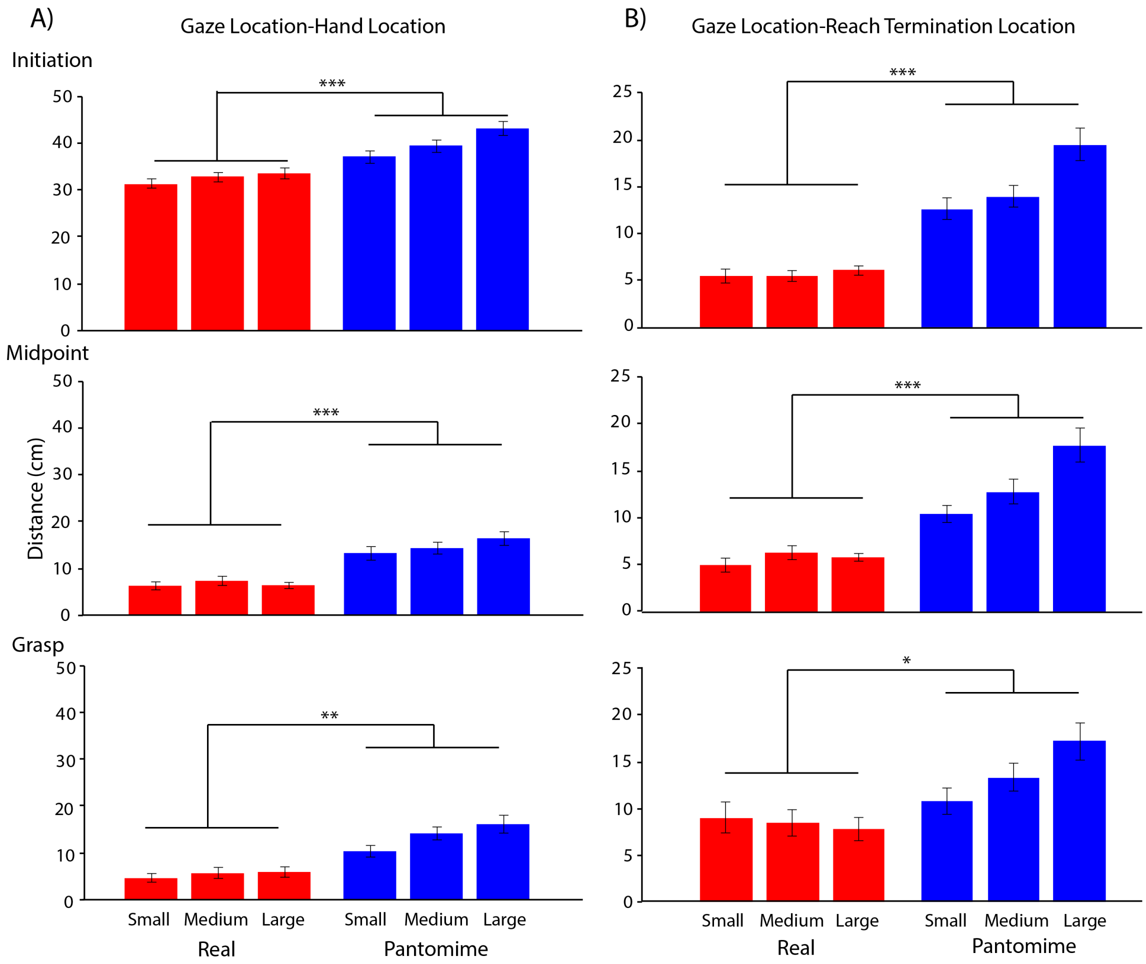


Figure 2.8. Gaze Location Distance. A. Gaze Location - Hand Location Distance. Average absolute distance from point-of gaze coordinate to digit midpoint coordinate (mean ± standard error). B. Gaze Location- Reach Termination Location Distance. Average absolute distance from point-of gaze to reach termination point. For the real (red) and pantomime (blue) condition at three time points: A) Initiation, B) Midpoint, and C) Grasp. (*p<0.05, **p<0.01, ***p <0.001)

Figure 2.8B shows that during the real task participants visually fixated on the target at all points during the reach, but there was no similar fixation on the virtual target in the pantomime task. An ANOVA on gaze to target distance confirmed that the distance was smaller for the real reach vs the pantomime reach task, Task, $F(1,16) = 19.306$, $p < 0.001$. There were also significant main effects of Time, $F(2,32) = 1.237$ $p = 0.304$, and Size, $F(2,32) = 9.182$, $p = 0.001$. Further, there were significant interactions of Time x Task $F(2,32) = 12.802$, $p < 0.001$ and Task by Size $F(2,32) = 5.407$, $p = 0.009$. Pairwise analyses revealed that the fixation to target distance for the small ball was smaller ($p = 0.001$) from the medium ball ($p = 0.002$). Taken together, these results suggest where as participants in the real condition were looking at the real target, only some of the participants in the pantomime task, and mainly for the small ball, were directing their gaze toward the virtual location of the target, and then only toward the end of the reach.

2.7 Discussion

This study compared gaze anchoring and hand shaping movements associated with real reach-to-grasp movements, reaching for a ball of one of three different sizes located on a pedestal, and pantomime reach-to-grasp movements, pretending to reach for one of the target balls on a pedestal, with the ball and pedestal absent. When making real reaches, participants visually fixated the target as the reaching movement was initiated and disengaged visual fixation of the target at about the point that the target was grasped, a behavior that is referred to as gaze anchoring. Gaze anchoring was absent in the pantomime reach task. Real reach-to-grasp movements also featured kinematic measures of the reach, i.e.; maximum height, maximum pre-grasp, and grasp that were proportional to the size of the target. Pantomime reaches featured kinematic measures for the reach in which scaling did not reflect the actual target size. Furthermore, during pantomime movements, gaze was not systematically related to the previous location of the target, the virtual location of the target as defined by the point that a participant made a grasping movement, or the participant’s hand. The presence of gaze anchoring during real-reach-to-grasp is consistent with the action-perception theory that proposes that real visuomotor action is mediated via dorsal stream online control. The absence of gaze anchoring during pantomime reach-to-grasp is consistent with the action-perception theory proposal that pantomime is mediated by off-line control.

The present study supports previous work showing that the reach trajectory and hand shaping movement associated with a pantomime reach is different from that associated with a real reach (Goodale et al. 1994; Westwood et al. 2000; Fukui & Inui 2013b; Holmes et al. 2013; Kuntz & Whishaw 2016). Here we found that a pantomime reach featured a peak height that was larger than that of real reach, a peak aperture (maximum pre-grasp) and minimum aperture (grasp) between the first two digits that was smaller than that of a real grasp, and a movement duration that was shorter than that of a real reach. In addition, the variability in the kinematic measure of pantomime reaches was greater than that of real reaches. In general, that there are kinematic differences between real reaches and pantomime reaches, is consistent with the original finding of Goodale et al. (1994).

Nevertheless, previous work has also shown that pantomime movements are influenced by visual contextual cues (Gentilucci et al. 1996; Coats et al. 2008; De Stefani et al. 2014; Kuntz & Whishaw 2016). For example, in a task in which participants reach for a food item located on a pedestal, kinematic measures are different depending upon whether the participants pantomime with the pedestal displaced, absent, or pantomime without vision (Kuntz & Whishaw 2016). Therefore, it might be expected that kinematic differences in real and pantomime reaching will vary from experiment to experiment in concert with contextual differences. The pedestal was removed in the present study, because its presence, although requiring a pantomime grasp, would nevertheless provide a target for the reach. In this respect, the task would be a pointing task, in part, and pointing tasks have been shown to feature gaze anchoring (Neggers & Bekkering, 2000; Prablanc, Echallier, Jeannerod, & Komilis, 1979). All of the other room cues were unchanged for the real and pantomime tasks and the subjects were sighted. Therefore, in general, the test situation and the kinematic results are sufficiently similar to test situations used in previous work to make a rigorous comparison of the gaze activity associated with real and pantomime reaches.

Gaze anchoring associated with real reaches for balls in the present study was similar to that reported in previous work for participants reaching to grasp a food item (de Bruin et al. 2008; Sacrey & Whishaw 2012b). For a real reach, a saccade moved visual fixation to the target as the reach was initiated and then, about the time of the grasp, visual fixation on the target was disengaged, often with a blink and head movement. Gaze anchoring was not observed during pantomime reaches, as there was little systematic change in gaze direction from before the initiation of the reach until after the grasp was completed. Whereas for real reaches, the variance in eye fixation relative to the pedestal surface decreased to its lowest values in the second third of the reach, there was no such systematic change in variance during pantomime reaches. To further investigate whether gaze in pantomime reaches was systematically directed to any target, including a participant's reaching hand or the virtual location of the target they were reaching for, measures were made of gaze direction relative these targets. Although some participants clearly looked at their hand at some point during the reach and other subjects looked toward the virtual target that they were grasping, it was clear that there was no systematic relation of gaze to these targets. Indeed, inspection of gaze in individual subjects suggested that the gaze direction for each participant could change during the reach and was dissimilar across participants and even dissimilar from trial to trial. Taken together, gaze anchoring is absent in any form during pantomime reaching.

Substantial evidence proposes that a reach-to-grasp is the composite of two separate movements, a reach and a grasp, each mediated by a different anatomical pathway from visual cortex through the parietal cortex to the motor cortex (Arbib 1981; Jeannerod 1981; Jeannerod et al. 1994; Culham & Valyear 2006; Cavina-Pratesi et al. 2010b; Karl et al. 2013). It is likely that gaze anchoring contributes to some feature of online integration of the reach and the grasp because if vision is altered by blindfolding or asking a participant to reach for a target in peripheral vision, the reaching movement decomposes, with the reach occurring first to locate the target and the grasp following in response to tactile information obtained from touching the target (Karl et al. 2012; Hall et al. 2014). Although the participants in the present pantomime task were sighted, the results suggested that they made little functional use of vision in relation to their pantomime reaches. Nevertheless, their pantomime movements did reflect experimental contingencies. They did direct their reaches in the general direction of the pedestal’s previous location and they did make larger hand shapes for larger targets. Their ability to pantomime a semblance of both the reach and the grasp is likely due to their previous experience with reaching for the different sized balls and to the instructions that requested that they reach for a ball of a particular size, memory features that depend upon perceptual mechanisms.

A number of experiments have attempted to normalize pantomime reaching, mainly by providing the participant with tactile information about the size of the target (Bingham et al. 2007; Chan & Heath 2017; Jazi & Heath 2017; Rinsma et al. 2017). It is also clear from other work that even when participants reach without vision they begin to make more accurate maximum pre-grasp hand shapes for a target if they are able to learn about target features by touching the target a number of times (Karl et al. 2013). Further, magicians who are professionals at using sleight-of-hand, perform similar real and pantomime reach-to-grasps as long as the target has only been displaced and not removed entirely, which also suggests that practice may improve pantomime kinematics (Cavina-Pratesi et al. 2011). Given that gaze anchoring is a feature of real reaching, it seems possible that were participants given instructions with respect to the use of vision during pantomime; e.g., by asking them to look, or giving them training in looking, their performance may come to more closely resemble real reaching. This possibility could be investigated in future studies. Nevertheless, perhaps the more relevant question is whether improving pantomime measures through experiential or instructional commands will shift pantomimes performance to neural substrates that are more similar to those which mediate real reaching. This question could only be answered by experimental investigation using brain imaging techniques concurrently with uninstructed and instructed pantomime reaches.

The present study is relevant to other aspects of the relationship between gaze anchoring and reaching movements. Neggers & Bekkering (2000) have discussed the possible relationships between the neural control of both attentional saccades and reaching movements. They suggest that there is an obglitory relation between arm movements and visual saccades. The present study, by demonstrating that pantomime reaching movements are not associated with gaze anchoring suggests that any obligatory relationship depends upon the presence of a visual target. Although the neural basis of the coupling of gaze anchoring and reaching is uncertain, Neggers & Bekkering (2000) also review evidence that suggests a role for superior colliculus projections into the cortical dorsal stream in gaze anchoring. Indeed, the monkey Helen who had received a bilateral primary visual cortex removal is reported to display gaze anchoring when reaching for food items (Whishaw et al. 2016). With respect to this idea, a simple distinction between real and pantomime reaching is that the former involves collicular mediation and the latter does not. In this respect, the present findings are also consistent with the idea that the neural basis of exogeneous (bottom up) vs endogeneous (top down) attentional processes (Posner 1980; Casarotti et al. 2012) may be dissociated with respect to subcortical vs cortical sensory guidance. The present results show that whatever neural processes may be involved in generating a pantomime reach movement that resembles a real reaching movement, in that a fascimily of both the reach and grasp are present, those processes need not concurrently evoke a fascimile of gaze anchoring eye movements.

In conclusion, substantial evidence supports the idea that pantomime reaching, as an intransitive action, is a largely visually independent action. This idea is supported by combined fMRI/DTI imaging of imitative, imagined, and pantomime movements (Vry et al. 2015; Goldenberg 2017). These studies suggest that a ventral parietal/frontal pathway represents the imagined target whereas a temporal/frontal pathway independent of visual cortex represents the pantomime movement. Collectively, the current study highlights the differences in visual attention in real and pantomime grasping movements. Furthermore, this study shows that online visual guidance is essential and tightly coupled to real reach-to-grasp movement, whereas, when a reach-to-grasp movement is completed in the absence of a real target, hand and eye movements are uncoupled. Based on these results, we concur that the differential task demands of real vs pantomime reaching evoke different neural systems, a central tenant of the action-perception theory (Milner & Goodale 2006).

Chapter 3

Contextual Cues Dissociate Reach and Grasp by Altering Gaze Anchoring for Pantomime: Further Support for the Dual Visuomotor Channel Theory of Reaching

3.1 Abstract

A pantomime reach-to-grasp movement is different from a real reach-to-grasp movement in time to completion, peak velocity, maximum pre-grasp aperture (MPA), and grasp aperture (GA). Whereas vision is critical to a real reach-to-grasp, with gaze anchored on the target throughout the movement, gaze is not systematically related to pantomime reaches. Nevertheless, pantomime reaches vary as a function of the contextual conditions in which they are performed and there has been no examination of whether gaze might also vary as a function of the context in which pantomime reaches are performed. This question was examined in the present study by examining gaze points during a real reach-to-grasp and a pantomime of the same movement in three different contexts. Participants reached-to-grasp either a small chewable candy (skittle®) or a larger round donut ball from a pedestal placed in front of them with the purpose of eating it or pantomimed the same movements with: (1) the pedestal present, (2) the pedestal present but its location shifted, or (3) the pedestal absent. Confirming previous work, real reach-to-grasp MPA and GA were smaller in all pantomime contexts than real reach-to-grasp. As expected, gaze anchoring, defined as the focusing of gaze on the target from initiation until about the time of the grasp, occurred with real reaches. It also occurred in the pantomime condition, but only when the pedestal was present, not when it was displaced or removed. That gaze anchoring is associated with both real and pantomime

reaches that involve a target is discussed in relation to the support that it provides for the dual visuomotor channel theory, that reaching consists of two component movements, a reach and a grasp. Pantomime performed with the pedestal present dissociates the components such that the reach is real and the grasp is pantomimed.

3.2 Introduction

Reaching out to grasp objects such as food items that are to be placed in the mouth for eating, is an everyday action. The dual visuomotor channel theory proposes that the act is a composite of two movements, a reach and a grasp, each of which is subserved by different visuomotor pathways through parietal to motor cortex (Arbib 1981; Jeannerod 1981; Jeannerod et al. 1994). The reach involves proximal control of musculature that directs the hand to the target in relation to the extrinsic (location) properties of the target. The grasp involves more distal hand shaping movements to orient and shape the fingers for target purchase relative to the intrinsic (size, shape) properties of the target. The online visual control of reaching is evidenced by its association with gaze anchoring. At about the initiation of a reaching movement, an eye saccade directs gaze to the target and gaze is only disengaged by blinking or looking away at about the time the target is grasped (Prablanc et al. 1979; de Bruin et al. 2008; Sacrey & Whishaw 2012b). The function of gaze anchoring may be to integrate the reach and the grasp into a seamless action in relation to the target. In support of the idea that gaze anchoring is central to integrating the reach and the grasp, when reaching without vision or into peripheral vision, the reach and the grasp are dissociated: the reach is used to find the target, after which the grasp is calibrated using touch cues (Karl et al. 2013; Hall et al. 2014). Furthermore, when a participant is asked to pretend to make a reach-to-grasp movement, the pantomimed kinematics of the reach and the grasp are altered (Goodale et al. 1991; Goodale et al. 1994; Westwood et al. 2000; Milner et al. 2001; Fukui & Inui 2013a; Holmes et al. 2013; Kuntz & Whishaw 2016). The pantomime reach-to-grasp action has an altered peak velocity, altered maximum pre-grasp aperture, and an altered grasp aperture. There is also no systematic relation between gaze and the endpoint of the pantomime reach movement or its grasp (Kuntz et al. 2018). Such differences between real reach-to-grasp and pantomime reach-to-grasp is support for the idea that the former is performed online via the dorsal stream visuomotor pathways and that the latter is performed offline via ventral stream visuotemporal pathways (Milner & Goodale 2008).

Despite the finding that gaze anchoring is not associated with pantomime reaching, pantomime actions do vary in relation to the context in which they are performed. Depending upon contextual conditions in which a pantomime action is performed, the reach and the grasp might be altered in different ways (Berkinblit et al. 1995; Gentilucci et al. 1996; Bingham et al. 2007; Coats et al. 2008; Karl et al. 2013; De Stefani et al. 2014; Kuntz & Whishaw 2016; Chan & Heath 2017; Jazi & Heath 2017; Rinsma et al. 2017). In the seminal demonstration of kinematic differences in real and pantomime reaching, Goodale et al. (1994) removed the target object for the pantomime condition but the context, including the table on which the target object had been placed, was unchanged. Thus, the configuration of the table with respect to the room and the participant could provide extrinsic cues to guide the pantomime reach to the place at which the target had been placed. Both human and nonhuman animals are adept at navigating to a place after a cue marking its location has been removed (Whishaw et al. 1995; Astur et al. 1998). In support of the idea that contextual cues influence pantomime reaching, Kuntz et al. (2016) report that both the reach and the grasp of pantomime reaching systematically become more different from a real reach-to-grasp as contextual cues related to the place at which the target of a real reach was located are removed. This result suggests gaze may similarly change in relation to changes in context and could thus reveal whether gaze is more closely linked to guiding the reach, shaping the grasp, or integrating the two movements. Understanding the relationship between real reaching, pantomime reaching and their visual control is important for investigating the neural basis of reach-to-grasp movements (Jeannerod et al. 1994; Binkofski et al. 1998; Culham & Valyear 2006; Cavina-Pratesi et al. 2010a; Cavina-Pratesi et al. 2010b; Vesia & Crawford 2012; Vesia et al. 2013; Ogawa & Imai 2016; Cavina-Pratesi et al. 2018; Singhal et al. 2013).

For the present study, participants in the real reach-to-grasp condition reached for a small and a large food target located on a pedestal directly in front of them. For the pantomime conditions, participants pantomimed the same reach under altered contexts: (1) the pedestal and food target present, (2) the pedestal with the food target in the center are present but shifted to one side, or (3) the pedestal absent. Eye movements were recorded with a head-mounted, video-based eye tracker while hand movements were recorded with electromagnetic sensors attached to the thumb, index, and wrist. This experimental set-up allowed simultaneous recordings to establish where participants look as the reach-to-grasp actions progressed.

3.3 Materials and Methods

Participants

Participants were 23 right-handed young adults (11 male, 12 female; mean age 19.95 ± 0.9 years) recruited from Thompson Rivers University introductory psychology classes and received class credit for their participation. Participants were randomly placed into one of two experimental groups. Each participant gave informed consent, authorized use of photos or videos, were self-reported as having no history of neurological, sensory, or motor disorders as well as normal, or corrected-to-normal, visual acuity. The University of Lethbridge and Thompson Rivers University, Human Subject Research Ethics Committees approved the study.

Test situation

Participants were seated in a brightly lit room with a self-standing height-adjustable pedestal placed in front of them. The pedestal was placed at a horizontal reach distance normalized to the participant's arm length (100 % of the length from the shoulder to the tip of the index finger with the elbow at 180° flexion) and the height of the pedestal was adjusted to the participant's trunk height, with 100 % of height from floor to outstretched arm while seated with the arm-shoulder at 90° flexion (Whishaw et al. 2002). This experimental setup allowed participants to naturally reach with their right hand towards the pedestal to pick up the target.

Video recording

Two video cameras recorded behaviour throughout the experiment. Filming was performed at a sampling rate of 30 Hz and 1/1000 shutter speed with cameras placed to capture both frontal and sagittol views.

Hand kinematics

Thumb, index, and wrist movements were acquired at a sampling rate of 60 Hz using a trakSTAR® (Ascension Technology Corporation) system. The position of the digits and wrist were calculated from electromagnetic sensors placed on the participant's hand; two on the distal phalanges of the thumb and index finger, and one on the wrist on the anterior aspect of the ulnar styloid, with respect to the transmitter. The transmitter was fastened to the floor beneath the participant's right chair legs such that the transmitter and the hand's start position were vertically aligned.

Eye movement

Eye movement was recorded using a ViewPoint EyeTracker® (Arrington Research, Inc.) a monocular scene-based eye-tracking device. Eye-tracking glasses were worn for the entirety of the experiment and collected data at a sampling rate of 30 Hz. A sixteen-point eye calibration was performed prior to data collection and was adjusted if necessary during the experiment (when there was a significant drift between gaze-point and the target to be fixated).

3.4 Procedure

In the experiment two target objects were used. A subset of the participants (n=13) reached for skittles, a candy with approximate diameter of 8.25 mm and the remaining participants (n=10) reached for a round donut ball with a diameter of approximately 28.82 mm. Participants were seated in a comfortable upright position with feet flat on the floor with hands placed in the start position. The start position for the right hand was marked by a piece of tape on the thigh, and participants started with their thumb and index finger in opposition. The left hand was resting in an open and relaxed position on the thigh. Participants were then presented with a set of practice trials where they reached out and grasped an object and brought it back to their chest. This was done so that participants would not only be accustomed to the task, but to ensure that the equipment would not interfere with their natural reach-to-grasp movement. Participants adopted the start position between trials and waited for a start prompt which was a verbal “1-2-3- GO” command from the investigator. The experiment consisted of four contexts illustrated in Figure 3.1.

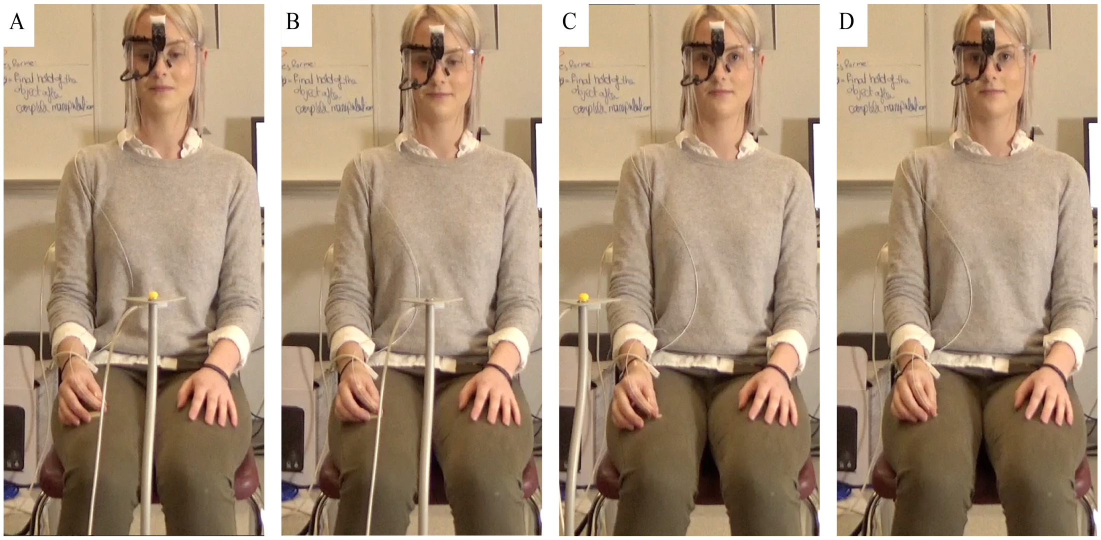
(1). Real reach. Pedestal and target present. For the real condition, participants were instructed to “reach out and grasp the target and bring it back up to your mouth as if to eat it”.

(2). Top pantomime. Pedestal present and target absent. The participants were instructed to “ pretend to reach out and grasp the target object as you did when the target was present.”

(3). Beside pantomime. Pedestal and target present but shifted to the left 7.62 cm. The participants were given the same instructions to pantomime the movement.

(4). Complete pantomime. Pedestal and target absent. The participants were given the same instructions to pantomime the movement.

In each context, participants performed three reaches (Karl et al. 2013). All reaches for the real condition were completed prior to the pantomime condition to ensure that all participants were familiar with the real condition before they performed the pantomime conditions.



Real Top Beside Complete

Figure 3.1. Real and Pantomime reaching contexts. A) Real, target is on the pedestal. B) Top, pedestal is present but target is absent, C) Beside, pedestal and target is displaced to the right side of its previous location. D) Complete, neither the pedestal nor the target is present. In all conditions participant reached from the lap to pick up (context A) or pantomime (contexts B-D) picking up the target object to bring it back to their mouth for consumption.

Hand movement kinematics

Kinematic events were processed using custom-written algorithms created in Matlab® (Version R2016b; The Mathworks, Natick, MA, USA). A participant made a lateral movement with the reaching hand before they placed the hand in the start position with the first two digits in opposition. Movement initiation was defined as a minimum wrist velocity threshold of 5 mm/sec in the frontal direction after the 1-2-3- GO command. Withdraw was defined as occurring after the grasp and constituted a backwards movement of the hand toward to the body. The reach-to-grasp movement then consisted of measures between reach initiation to withdraw. Kinematic measures determined from the data consisted of the following:

> *(1). Maximum pre-grasp.* Maximum pre-grasp aperture (MPA) was defined as the maximum index-thumb aperture obtained between movement initiation and grasp.
>
> *(2). Grasp aperture.* Grasp aperture (GA) was defined as the minimal closing aperture between the index finger and thumb, prior to the beginning of the withdraw movement.

Gaze Direction

Participant visual fixations, relative to the visual scene in front of them, were analyzed using Point Picker (ImageJ, Natick, MA, USA). In the Real reach context, relative gaze measures were calculated from 8 points that were identified by stepping through the visual fixation data frame-by-frame. The 8 points were the tips of the thumb and index finger, the three corners of the pedestal, the fixation point, and the center of the target. For the pantomime reach conditions, 4 points were identified: tips of the thumb and index finger, the tripod block of the camera positioned in front of the participant, and the fixation point. Sometimes the eye tracker lost track of the eye, due to blinks, eyelash interference, or other unknown factors. If the eye tracking was lost at an abnormal rate on multiple trials across reach scenarios data from that participant was discarded; therefore, eye movement results are derived from 17 subjects (Skittle N=10; Donut N=7). The location and duration of visual fixations were derived from these measures.

(1) Gaze point. Measures of gaze point, the point indicated by the eye tracker of where a participant was looking, were taken at three different time points for each reaching trial: Movement initiation, Midpoint of hand transport, defined as 50% of reach duration, and Termination of reach, signified by a grasp. The measure was the distance between the

gaze point relative to the center of the pedestal. The mean position of the center of the pedestal in the real condition was used to define the location of the “center of the pedestal” in the pantomime conditions in which the pedestal was moved or was absent.

(2) Gaze trajectory. To calculate gaze focus during each trial, two distance measures were made on each frame: 1) Distance of gaze point relative to the center of the pedestal (Gaze Point-Pedestal). 2) Distance of gaze point relative to the midpoint between the thumb and index (Gaze Point-Hand). Measurements began 10 frames prior to reach initiation and ended 10 frames after grasp completion. Individual data were interpolated to plot average visual trajectory in relation to reach time.

(3) Duration. The duration of the reach-to-grasp movement was measured from the point of first movement of the hand to the point of the first withdraw movement after the grasp.

Statistical Analysis

The data were analyzed using repeated-measures analyses of variance (RM-ANOVA) with the statistical program SPSS (v.24.0.0). A p value of < 0.05 was considered significant. Results are reported as mean ± standard error.

Hand kinematics. Data from the skittle and donut targets were analyzed both individually and grouped. This resulted in three different ANOVAs. The individual analysis for each target had Context (Real, Top, Beside, Complete) and Trials (1, 2, 3) as the within-subjects factors. The third ANOVA had the same within-subjects factors with the addition of between-subjects factors of Target Size (Skittle, Donut).

Gaze point. Data from the skittle and donut targets were analyzed separately for the time of Initiation, Midpoint, and Grasp in three different ANOVAs with Context (Real, Top, Beside, Complete) and Trial (1,2,3) as within-subject factors. Gaze point data was further analyzed by running a separate ANOVA for each target with Time (Initiation, Midpoint, Grasp) and Trials (1,2,3) as the within-subject factors.

Gaze trajectory. The distance measurement between the gaze point relative to the pedestal and relative to the hand were the dependent variables. Data from the Donut and Skittle were analyzed in separate ANOVAs for each dependent variable (4 ANOVAs) with Context (Real, Top, Beside, Complete), Time (1-30) and Trials (1, 2, 3) as the within-subjects factors.

Duration. A single ANOVA for the dependent measure of reach duration had Target size (Skittle, Donut) as a between-subjects factor and Context (Real, Top, Beside, Complete) and Trials (1, 2, 3) as the within-subjects factors.

3.5 Results

For all Contexts, RM-ANOVA's indicate that there was no effect of trials and so only effects related to the test conditions are reported.

Maximum pre-grasp aperture

Figure 3.2 illustrates the mean MPA for the real reach-to-grasp and pantomime reach-to-grasp conditions with the skittle (top) and donut (bottom) as the target. MPA was larger for the donut than for the skittle for both the real and the pantomime contexts. This was confirmed by a an overall analysis which revealed a significant effect of Target Size, $F(1,20) = 63.717$, $p < 0.001$. There was no effect of Context, $F(3,60)=2.594$, $p=.061$, but there was a significant Target Size by Context interaction, $F(3,60)=8.416$, $p<0.001$.

For the skittle target (Figure 3.2-top), there was a significant effect of Context $F(3,36) = 8.420$, $p < 0.0005$. Post-hoc analyses indicated that the MPA in the Real reach-to-grasp context was not different than in the Top pantomime contexts, but both were smaller than in the Beside and Complete pantomime contexts ($p<0.05$)

For the donut target (Figure 3.2-bottom), there was a significant effect of Context $F(3,) = 5.579$, $p = 0.004$. Post-hoc analyses indicated that the MPA in the Real reach-to-grasp context was greater than in the three pantomime contexts ($p<0.05$)

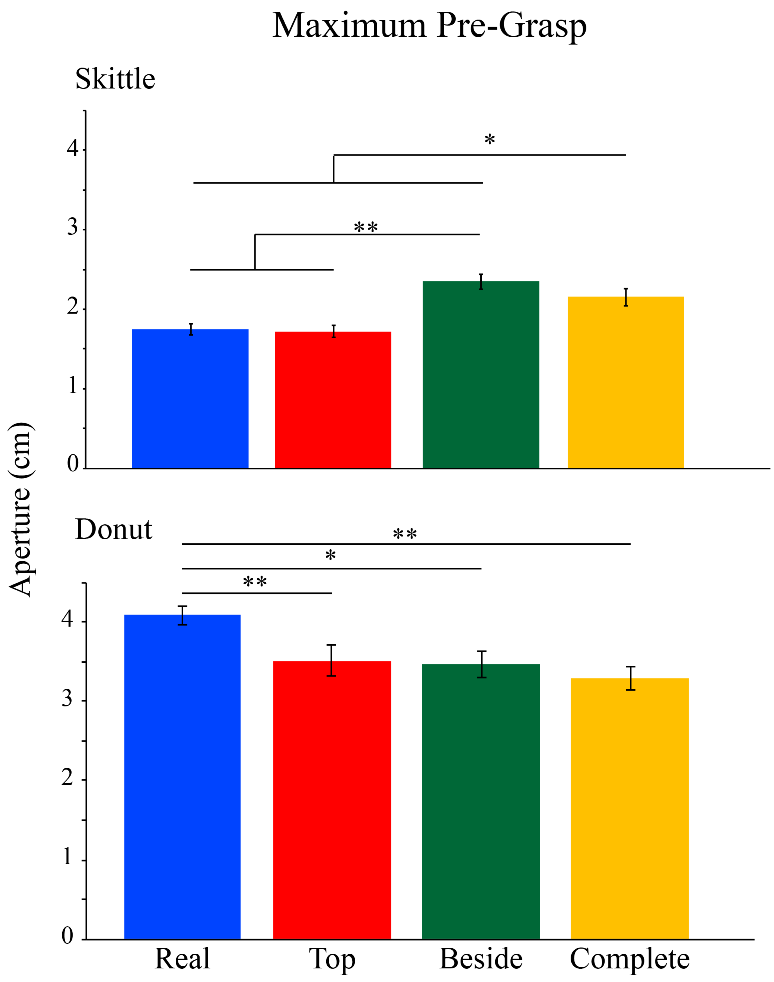


Figure 3.2 Maximum pre-grasp aperture (mean ± standard error) for skittle (top) and donut (bottom) targets. *Note*: Maximum pre-grasp aperture is smaller for the skittle than for the donut and that the MPA for the real contexts differs from their pantomimes (*p<0.05, **p<0.01).

Grasp aperture

Figure 3.3 illustrates mean GA as a function of context for the skittle (top) and donut (bottom) targets. GA was larger for the donut target than for the skittle target and GA for the pantomime contexts differed from the Real reach-to-grasp context. This was confirmed by a between subject factors comparison which revealed a significant effect of Target Size, $F(1,20) = 15.527$, $p < 0.001$. There was also a significant effect of Context, $F(3,60)=22.95$, $p < 0.001$, and an interaction of Target Size by Context, $F(3,60)=9.42$, $p < 0.001$.

For the skittle target (Figure 3.3-top), there was a significant effect of Context, $F(3,36) = 4.623$, $p = 0.008$. Post-hoc analyses indicated that there was no GA difference in the Real reach, Top pantomime, or Beside pantomime contexts, which were all significantly larger than the GA in the Complete pantomime context ($p<0.05$).

For the donut target (Figure 3.3-bottom), there was a significant effect of Context, $F(3,27) = 17.377$, $p < 0.0005$. Post-hoc analyses indicated that GA was significantly larger for the Real reach context than for all pantomime contexts ($p<0.01$).

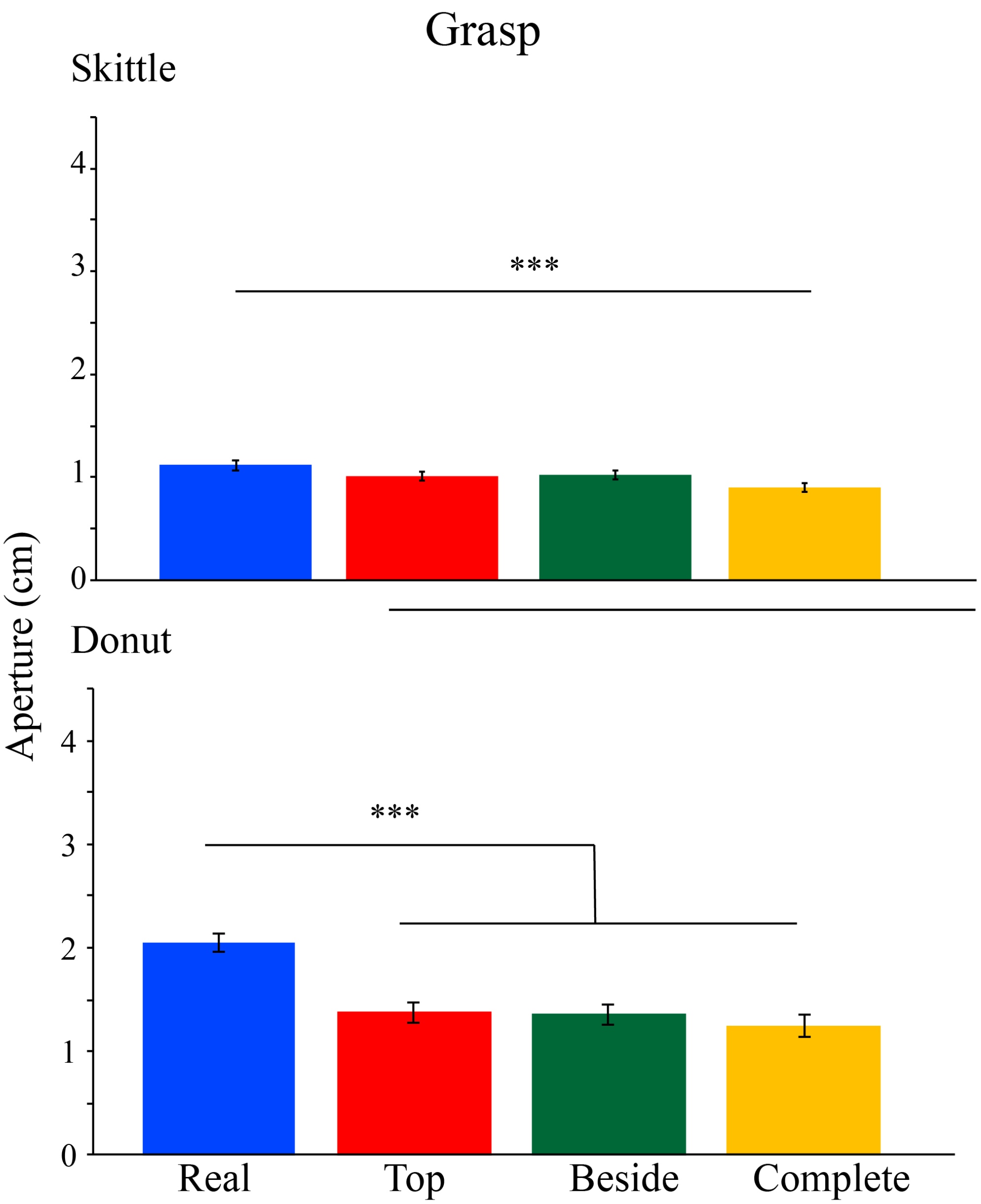


Figure 3.3 Grasp aperture (mean ± standard error) for skittle (top) and donut (bottom) targets. *Note*: Overall, grasp aperture is smaller for the skittle than the donut target (***p <0.001).

Hand distance to target

Figure 3.4 illustrates the minimum distance between the hand and the pedestal at the time of grasp completion (GA). An overall analysis including both targets found that minimum distance did not differ based on Target Size, $F(1,15) = 1.750$, $p = 0.206$, but there was a significant effect of Context, $F(3,45) = 20.132$, $p < 0.001$ and a significant Context by Target Size interaction, $F(3,45) = 3.519$, $p = 0.022$.

For the measure of minimum distance between the hand and the pedestal for the skittle target (Figure 3.4-top), there was a significant effect of Context $F(3,27) = 15.051$, $p < 0.001$. Post-hoc analyses indicated that the minimum distance for the Real reach context was not different from than that for the Top pantomime context, but both were smaller than the minimum distance for the Beside and Complete pantomime contexts ($p<0.01$).

For the donut target, the minimum distance from the hand to the pedestal (Figure 3.4-bottom), there was a significant effect of Context $F(3,18) = 32.267$, $p < 0.0005$. Post-hoc analyses indicated that the minimum distance observed for the Real reach context was not different than that for the Top pantomime context, but both were smaller than the minimum distance for the Beside and Complete pantomime contexts ($p<0.05$).

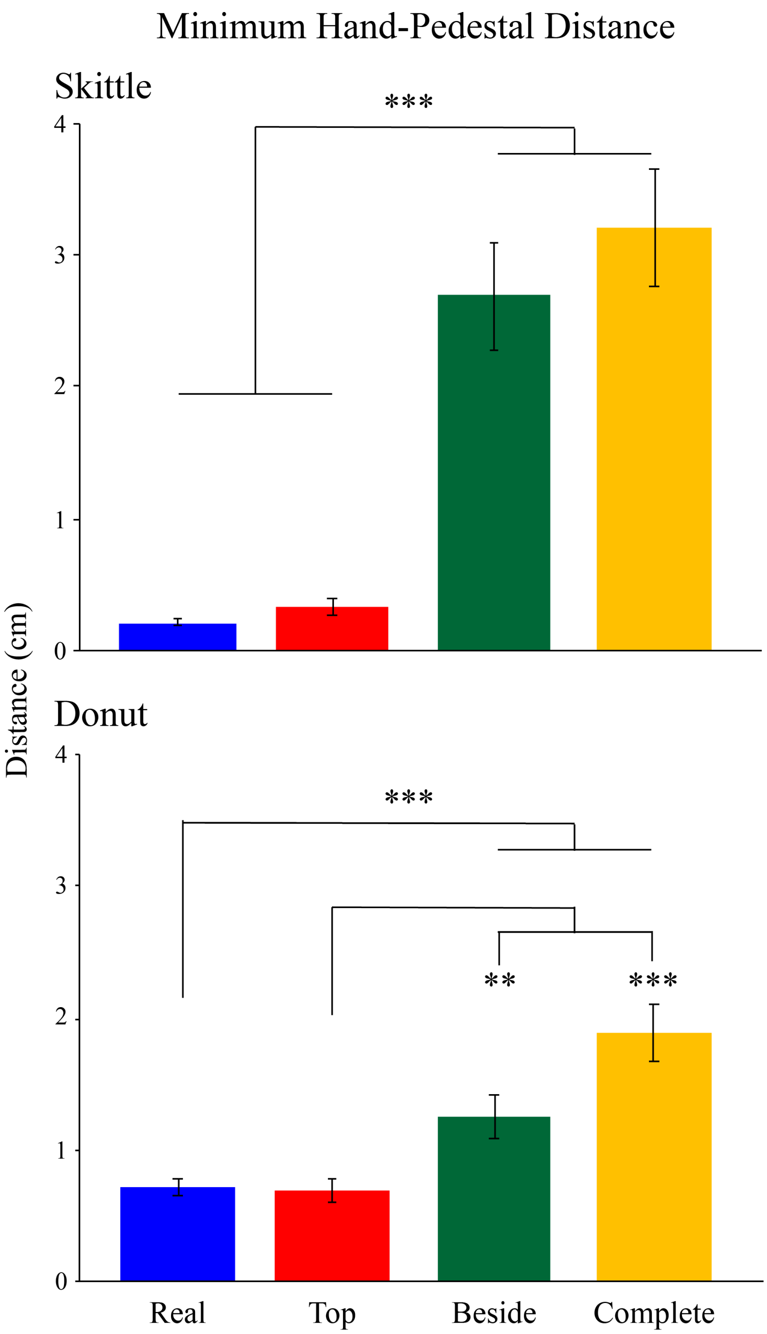


Figure 3.4 Minimum distance from hand to pedestal (mean ± standard error) for skittle (top) and donut (bottom) targets. *Note*: Minimum distance is smaller for both targets during the real and top pantomime contexts in comparison to the beside and complete pantomimes (**p<0.01, ***p<0.001).

Reach duration

The measurement of reach duration indicated that the reach for the skittle was longer than for that of the donut, Target size $F(1,15) = 6.216$, $p = 0.025$. Overall, reach duration was longer for the real than for the pantomime contexts, Context $F(3,45) = 5.932$, $p = 0.002$. There was no Context by Target Size interaction, $F(3,45) = 1.808$, $p = 0.159$.

Gaze point trajectory relative to the platform

The measurements of gaze point indicated that for both the skittle and donut, for all of the context conditions, gaze was directed in the direction in which a participant was to make the reaching movement. Figure 3.5 illustrates that by the midpoint of the reach, the gaze point of each participant was on the platform for both the Real reach and the Top pantomime contexts. For the pantomime Beside and Complete contexts, gaze points were not directed toward the platform’s previous location but were shifted away, mainly to the upper right of that location.

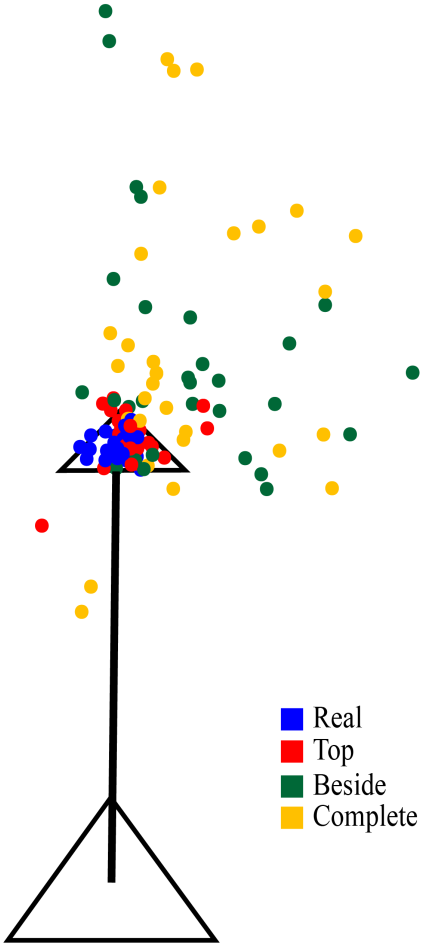


Figure 3.5 Point of gaze with reference to the pedestal at the reach midpoint for all participants and trials (skittle). *Note:* For the Real and pantomime Top context, gaze is directed to the pedestal whereas the pantomime Beside and Complete gaze is directed forward.

These conclusions were confirmed by an ANOVA that gave a significant effect of Context, $F(3,27) = 8.65$, $p < 0.0005$, Time, $F(2,18) = 4.15$, $p = 0.033$, and Context by Time, $F(6, 54) = 2.215$, $p = 0.055$. Post-hoc analyses confirmed that the distance from the gaze point to the pedestal was smaller for a real reach than for any of the pantomime contexts ($p<0.05$) but at the midpoint of the reach the Real and pantomime Top contexts were not significant (see Figure 3.6).

Donut. Figure 3.7 shows the average distance between gaze point and the pedestal in each context at the three time points (Initiation, Midpoint, and Grasp) for the donut target. The average measures showed that the gaze point was directed to the target for both the Real context and the Top context by the midpoint of the reach. A similar pronounced shift in gaze toward the pedestal's previous location did not occur for the Beside and the Complete contexts.

These conclusions were confirmed by an ANOVA that gave a significant effect of Context, $F(3,18) = 38.88$, $p < 0.0005$, but not Time, $F(2,12) = 1.319$, $p = 0.316$, or Context by Time, $F(6,36)=0.976$, $p=.456$. Post-hoc analyses confirmed that the distance from the gaze point to the pedestal was smaller in the Real context than for any of the pantomime contexts ($p<0.05$) but at the midpoint of the reach the Real and Top contexts were not significant (see Figure 3.7)

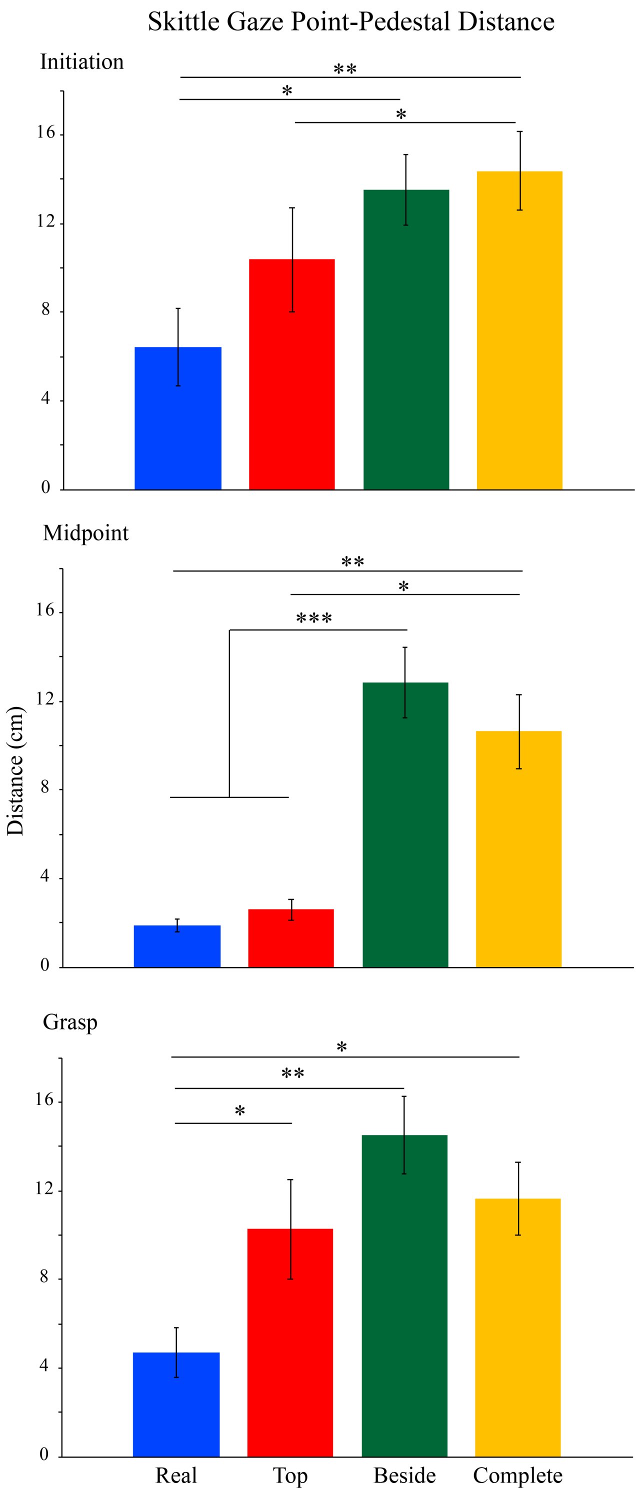


Figure 3.6 Gaze location distance from pedestal at three time points for the skittle target: Initiation, Midpoint, and Grasp for all contexts. *Note:* Gaze is more closely directed (anchored) to the pedestal at all time points for the Real context than for the pantomime contexts. (mean ± standard error **$p<0.01$, ***$p <0.001$)

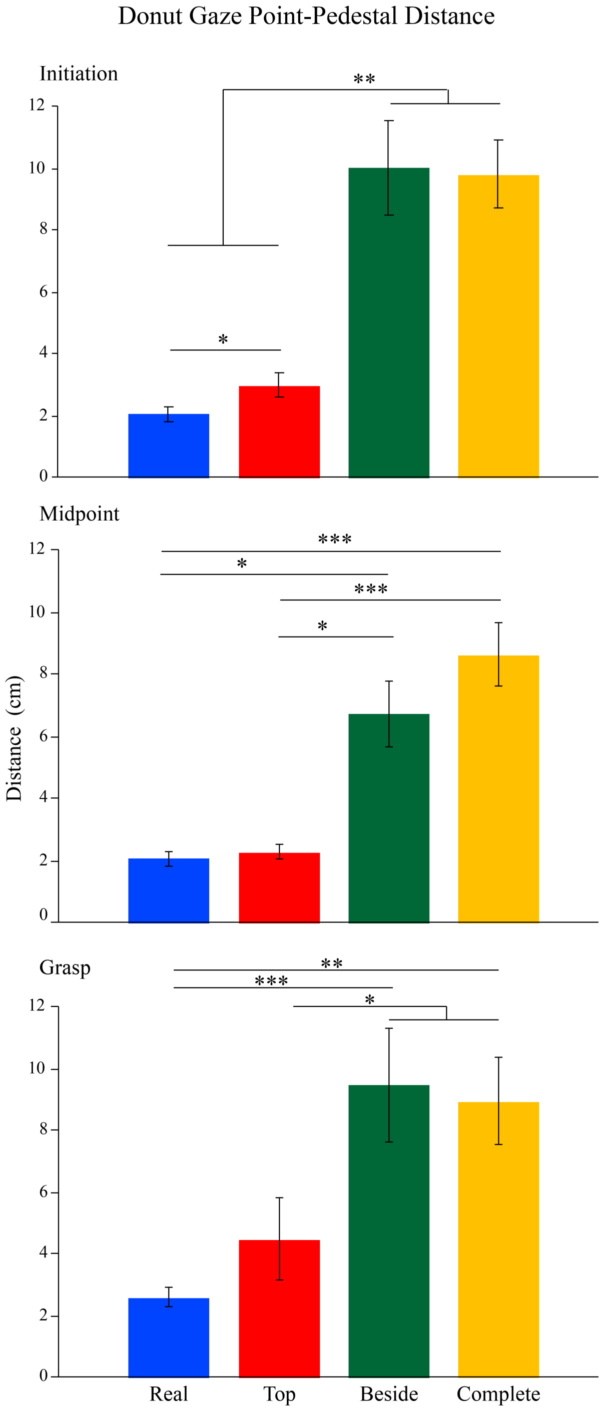


Figure 3.7 Gaze location distance from pedestal at three time points for the donut target: Initiation, Midpoint, and Grasp for all contexts. *Note:* Gaze is closely directed (anchored) to the pedestal at all time points for the Real context and at the midpoint for the pantomime Top Context than for the pantomime Beside and Complete contexts. (mean ± standard error *p<0.05, **p<0.01, ***p <0.001)

Temporal relationship between gaze point and the platform

Figure 3.8 illustrates the gaze trajectory throughout the reach-to-grasp movement relative to the platform for the skittle (top) and donut (bottom) targets. For both targets, gaze was shifted toward the location of the target at about reach initiation and shifted away from the target at about the time that the grasp occurred. The relative distance between the target and gaze point was similar in the Real reach and Top pantomime contexts, both of which featured shorter distances to the platform than did the Beside and Complete pantomime contexts.

These results were confirmed by significant differences in the distance between gaze point and the platform as a function of context for both targets: Skittle, $F(3,27) = 9.3008$, $p < 0.0005$ and Donut, $F(3,18) = 29.070$, $p < 0.0005$. Distances were significantly shorter for the Real reach context than for all the pantomime contexts when reaching for the skittle (Real reach vs Top pantomime: $p = 0.022$, Beside pantomime: $p = 0.001$, Complete pantomime: $p = 0.012$). In addition, for the skittle target, the distance between the fixation point and the pedestal for the Top pantomime context was shorter than for the Beside and Complete pantomime contexts ($p=0.016$). Similarly, post-hoc analyses for the donut target revealed that the distance between the fixation point and the pedestal were significantly different in the Real reach context compared to the Beside ($p=0.003$) and Complete ($p<0.001$) contexts. In addition, the Top pantomime context differed significantly from the Beside ($p=0.006$) and Complete ($p=0.000$) contexts.

There was also an overall effect of time point for both the Skittle, $F(52,468) = 7.906$, $p < 0.0005$ and Donut, $F(44,264) = 3.829$, $p < 0.0005$ targets along with a significant interaction for the skittle of Context by Time, $F(156,1404) = 1.782$, $p = 0.000$, and for the donut of Context by Time, $F(132,792) = 1.284$, $p = 0.024$. At reach initiation, indicated by time ‘0’ in the figure, participants look forward, but only in the Real and Top pantomime contexts does gaze anchoring to the pedestal occur.

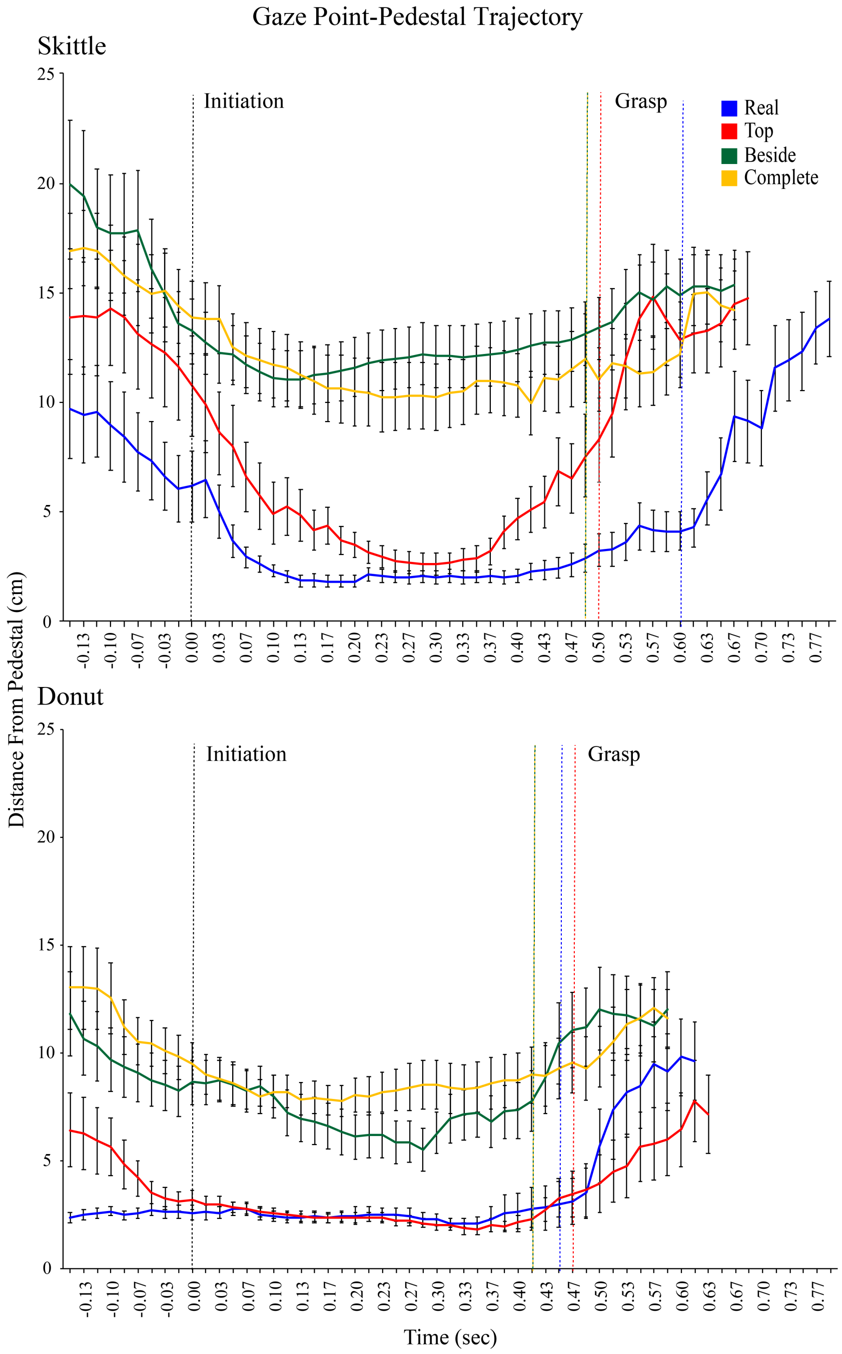


Figure 3.8 . Distance from the point of gaze to the center of the pedestal (mean ± standard error) throughout the reach-to-grasp movement for the skittle (top) and donut (bottom). *Note:* At reach initiation gaze is directed forward, but the shortest distance between gaze location and the hand occur for the Real and pantomime Top contexts and disengagement occurs earlier for the Top than the Real condition

Temporal relationship between gaze point and the hand

Figure 3.9 illustrates the gaze trajectory throughout the reach-to-grasp movement relative to the participant's hand for the skittle (top) and donut (bottom) targets. In all contexts, the gaze and the hand become more aligned as the reach proceeds but only in the Real and the Top contexts does the gaze focus on the hand as the reach is completed. These results indicate that the hand enters the field of view in all contexts but only in the Real and Top pantomime context does the hand approach the point at which gaze is anchored, which is the pedestal's location.

Thus, there was a significant difference between fixation point and the position of the reaching hand for both targets as a function of Context: Skittle, $F(3,27) = 3.698$, $p = 0.024$, and Donut $F(3,18) = 11.338$, $p < 0.0005$. Post-hoc analysis revealed that for both the skittle and donut targets the Real and Top pantomime contexts were significantly different from that of the Beside and Complete pantomime contexts ($p<0.05$). In addition, for both targets there was a significant effect of Time: Skittle, $F(52,468) = 67.947$, $p < 0.0005$, Donut, $F(44,264) = 166.528$, $p < 0.0005$) and a significant interaction of Context by Time: Skittle, $F(156,1404) = 1.672$, $p < 0.005$, and Donut, $F(132,792) = 1.945$, $p < 0.0005$.

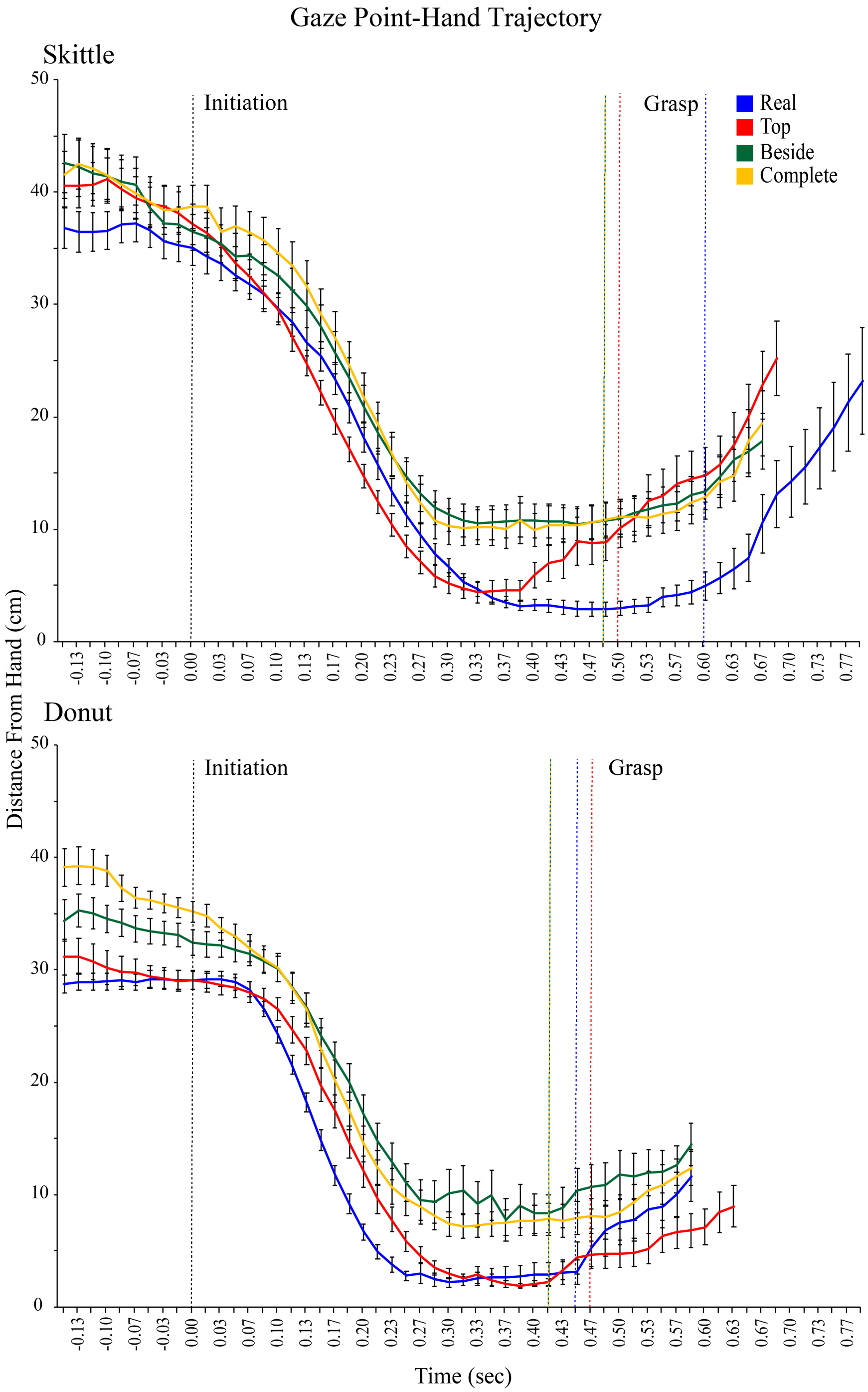


Figure 3.9 Distance from the point of gaze to the hand (mean ± standard error) throughout the reach-to-grasp movement for the skittle (top) and donut (bottom). *Note:* In all contexts the hand approaches the gaze location with the closest proximity for gaze location and hand location occurring for the real context.

3.6 Discussion

Because the kinematics of pantomime movements vary depending upon task context, the purpose of the present study was to examine whether gaze anchoring during pantomime also varies as a function of task context. Participants performed real reach-to-grasp movements for two different sized food items that were located on a pedestal, with the objective of placing the objects in the mouth for eating. They then pantomimed the same reaches with the pedestal present, the pedestal displaced to one side, or the pedestal absent. For real reach-to-grasps, MPA and GA and other kinematic measures varied as a function of food size and gaze was anchored on the target from about reach initiation to grasp completion. The kinematics of the pantomimed reaches and gaze points also varied as a function of the context. When the target was removed from the pedestal but the pedestal remained, the reach and gaze were both directed to the pedestal. When the pedestal was moved or removed, the reach and gaze were displaced from the pedestal's original location and were not closely related. The results show that gaze anchoring is associated with directing the hand to a target location whether or not the task is real or pantomimed. This finding suggests that gaze anchoring is more closely associated with the reach than with the grasp, a dissociation that supports the dual visuomotor channel theory, which posits that reaching is a composite movement containing a reach and a grasp.

A central finding of the present study is that gaze anchoring, which is featured in real reach-to-grasp movements, is present in the pantomime context when the pedestal is present but is absent in the two pantomime contexts in which the pedestal is not at its previous location. The interpretation of this result rests on the idea that a real reach-to-grasp movement is composed of two interlaced movements, each related to different stimulus features of the target. The reach is directed by the extrinsic properties of the target, the target's location, and the grasp is directed by its intrinsic properties, its size and shape. The present results suggest that when the target is removed for the pantomime context, but the pedestal on which it had been placed remains, the participants treat the pedestal as the appropriate place at which to make the pantomime grasp, even though they are not instructed to do so. That the participants treat the pedestal as the target of the pantomime reach is attested to by the similarity of grasp location in the real reach-to-grasp context and the pedestal pantomime context. It appears that for the pantomime context with the pedestal present, the movement of the hand toward the pedestal resembles pointing, a task that is also associated with gaze anchoring (Neggers & Bekkering 2000; Neggers & Bekkering 2001).

One way of viewing the results is that removal of the target objects in the pedestal pantomime condition successfully removes the intrinsic properties of the target, its size and shape, while not removing the target's extrinsic properties (location). The extrinsic properties of the target are only removed by additionally moving the pedestal upon which the target had rested. In light of this argument, in the pedestal pantomime context, the participants continue to make a “real” reach as measured by gaze anchoring and reach trajectory while at the same time making a pantomime grasp, as measured by alterations in MPA and GA. It is only when the pedestal is moved that the participants fully pantomime both the reach and the grasp. That the participants continue to treat the place that the target had been located as the proper place to pantomime, is not surprising. A substantial body of work shows that after humans and nonhuman animals are trained to navigate to a visible cue they still successfully and accurately navigate to that place after the cue is removed (Whishaw et al. 1995; Astur et al. 1998). Indeed, in previous studies of pantomime reaching, the place that the target had been placed was not altered and the participants pantomimed the reach in close proximity to the target’s previous location (Wong & Mack 1981; Goodale & Milner 1992; Goodale et al. 1994; Gentilucci et al. 1996; Bridgeman et al. 1997; Westwood et al. 2000; Goodale 2004).

The finding in the present study that pantomime reach-to-grasp movements differ with respect to gaze anchoring and hand shaping movements as context changes has several implications. First, the finding provides further dissociative support for the theory that the reach and the grasp are separate movements (Karl et al. 2012; Karl et al. 2013; Kuntz & Whishaw 2016). This finding adds to the other evidence obtained by the manipulation of vision (de Bruin et al. 2008; Karl et al. 2012; Sacrey & Whishaw 2012b), by anatomical studies (Whishaw et al. 2016), and by developmental and evolutionary descriptions of the movements (Sacrey et al. 2012a; Karl & Whishaw 2013; Thomas et al. 2014; Whishaw & Karl 2014). The findings also suggest that brain imaging comparisons of real and pantomime movements need to consider not only the context of reach and grasp movements but also the sensory control of the movements (Jeannerod et al. 1994; Binkofski et al. 1998; Culham & Valyear 2006; Cavina-Pratesi et al. 2010a; Cavina-Pratesi et al. 2010b; Vesia & Crawford 2012; Vesia et al. 2013; Ogawa & Imai 2016; Cavina-Pratesi et al. 2018). The present results show that only if the target and its location are removed does a complete pantomime of the reach and grasp occur.

The implication that gaze anchoring may be more closely tied to the reach than the grasp raises questions about how vision contributes to the grasp (Perry et al. 2016). Several observations suggest that gaze anchoring is not as closely related to the grasp as it is for the reach. Even though gaze anchoring is associated with real reach-to-grasp movements, visual disengagement frequently occurs before the target is actually grasped suggesting that vision is not essential to closing the digits on the target (Karl et al. 2012). Indeed, if a participant makes an error in purchase, the latency required to correct the movement using vision may be too long to be useful (Tao et al. 2018). In addition, even if participants cannot see a target, they quickly begin to shape their hands appropriately after only a few experiences in manipulating the target, showing that online visual monitoring is not necessary of calibrating MPA (Karl et al. 2013). It may be that a glance at some point in the reach is sufficient for achieving MPA and GA (Hu et al. 2005; Bingham et al. 2007; Kennedy et al. 2015; Tang et al. 2015; Davarpanah Jazi & Heath 2016; Heath et al. 2017; Goodman & Tremblay 2018). Thus, visual guidance of the reach may be different from visual guidance for the grasp. A number of studies also suggest that nonstriate visual pathways, such as the collicular-pulvinar pathway, may be involved in guiding the reach but not the grasp. For example, Neggers et al. (2001) suggest that a nonvisual signal such as the initiation of an arm movement recruits visual gaze for the reach. In addition, humans and nonhuman primates with striate cortex lesions gaze anchor and can reach for visual targets but are impaired in hand shaping when reaching (Milner & Goodale 2006 ; Whishaw et al. 2016), showing that non-geniculate-striate pathways can mediate the reach.

The present results provide further support for the idea that changes in the kinematic features of the reach and the grasp may vary with pantomime context (Kuntz et al. 2016). That the pantomime reaches were completed in less time than real reaches is consistent with findings by Wu et al. (2010), who observed that pointing movements that were completed under pantomime conditions had shorter overall movement times than real pointing movements.

As expected, a comparison of the time to complete the reach-to-grasp movement revealed that it was longer for the smaller skittle than for the larger donut (Castiello et al. 1993) and this time difference applied to both real and pantomime contexts. This finding is consistent with Fitts' Law, which predicts a longer reach time for smaller targets (Fitts 1954; Plamondon & Alimi 1997) and suggests that Fitt's Law is generalizable to pantomime tasks as well.

The present results show that hand shaping movements associated with a real reach-to-grasp movement are different than those associated with a pantomime reach-to-grasp movement, but also vary with pantomime context. Maximum pre-grasp aperture and grasp aperture are typically reported as smaller for pantomimed tasks than for real tasks (Goodale et al. 1994; Westwood et al. 2000; Fukui & Inui 2013b; Holmes et al. 2013; Kuntz & Whishaw 2016; Kuntz et al. 2018). In the present study, however, it was found that reductions in MPA and GA were more evident for the larger donut target than for the smaller skittle target. It is possible that there is a ceiling effect for detecting kinematic changes for an object as small as a skittle. Alternately, it may be that participants pantomime an average grasp aperture, such that small objects are overestimated and larger objects are underestimated. The present study also confirms that kinematic measures vary depending upon context because as contextual cues that indicate the location of the target decreased, larger divergence from the kinematics of the real reach-to-grasp movement was observed (Kuntz & Whishaw 2016). This finding is not surprising as previous studies of transitive (target cues present) and intransitive gestures (target cues absent) report they are different (Bonivento et al. 2014).

In conclusion, the present findings show that when participants pantomime a reach-to-grasp when the target itself is removed but the place upon which it was located remains, they direct their reach toward that place and their gaze is anchored on that place even though the kinematics of their hand shaping movements are altered. When they pantomime the movement in the absence of cues related to the target's previous location, their reach and gaze kinematics of their hand shaping movements are all altered. These results suggest that if place cues remain for a pantomime task, the reach and grasp are dissociated such that the reach retains features of a real reach while the grasp is pantomimed. This dissociation supports the dual visuomotor channel theory of reaching, which proposes that a real reach-to-grasp movements is a composite action featuring a reach and a grasp that are interlaced as a single movement.

Chapter 4

General Discussion

4.1 Introduction

Each day we interact with objects. We reach for objects, we grasp objects, and we manipulate objects to serve functions such as eating, playing, and working. It appears that these actions are relatively simple and occur with little to no planning for their execution this, however, is not the case. How these actions are produced is quite complex and involves multiple neural networks working in concert. To make matters even more complex, the neural networks that mediate real actions are not the same ones that mediate the pantomime of these same actions. The discussion will begin with a reiteration of the theories covered in the thesis, followed by a theoretical perspective of the results found in the thesis and how it pertains to past investigations, and finally close with caveats and future directions for this work.

4.2 Action-Perception Theory

In 1967, Schneider proposed that there were different systems that processed visual information: one stream for spatial orientation and another for pattern discrimination. This proposal was based from observations of feeding behaviour in hamsters. Namely, that when a sunflower seed is presented to a hamster, the hamster orients themselves in the direction of the seed prior to taking it. If the hamster is blind however, the seed must first make tactile contact with the whiskers before any orienting behaviour will occur. To take this one step further, Schneider performed the same food orienting procedure as well as a pattern discrimination task on hamsters who had complete bilateral ablations of the superior colliculi as well as on hamsters with visual cortex lesions. He found that the hamsters who had ablations to the superior colliculi lost their ability to orient to food that was presented in their visual field until it made tactile contact with the whiskers. These hamsters did however retain the ability to see visual stimuli as they showed a freezing response to visual stimuli and could discriminate between patterns. The hamsters with visual cortex lesions, though they were able to orient themselves to the sunflower seeds presented to them, failed to discriminate patterns.

These studies dissociated two distinct mechanisms for visual processing: the tectopulvinar system, which is comprised of the retina, superior colliculus in the tectum, pulvinar nucleus in the thalamus and the extrastriatal cortices and the geniculostriate pathway, which is comprised of the retina, lateral geniculate nucleus of the thalamus, and the striate cortex.

The tectopulvinar pathway is an evolutionary older system and in primates is functionally relied less upon than the geniculostriate pathway (Mishkin & Ungerleider 1982). Through lesion studies of Macaque monkeys, Miskin and colleagues revealed that the geniculostriate pathway could be functionally and anatomically separated into two extrastriatal visual streams that originate in the primary visual cortex (Mishkin et al. 1983). The two visual streams that originate from the geniculostriate pathway feed two visual streams. These streams were termed the ventral ‘what’ stream and the dorsal ‘where’ stream. This two stream hypothesis was modified nearly a decade later by Goodale and Milner (1992). They put forward that the dorsal ‘where’ pathway was now the ‘how’ pathway. This theory has subsequently received support from additional case studies (Goodale et al. 1994) and behavioral work (Pettypiece et al. 2010).

4.3 Dual Visuomotor Channel Theory

The dual visuomotor channel theory has its origins in observations of the organization of pointing movements. Woodworth (1899), described pointing as consisting of two phases: a ballistic movement that brings the forelimb to the general location of a target and a corrective movement guided by vision to position the hand at the target.

Prehension, the act of reaching out to grasp a target, was similarly described as consisting of two component movements: a reach and a grasp (Jeannerod 1981). This idea stems from observing that patients with a specific brain injury could no longer appropriately shape the hand for grasping. Despite their deficit in grasping behavior they remained competent at transporting their hand to the target. It was this observation, among other evidence, that lead to the dual visuomotor channel theory of prehension, which proposed that prehension was a temporally integrated movement consisting of two component movements, a reach and a grasp, mediated by separate neural pathways that transverse the parietal lobe from visual to motor cortex (Arbib 1981; Jeannerod 1981).

An important distinction of this theory is that it describes prehension in ethological terms. Namely, that the reach component is directed towards the extrinsic properties of the target (location, orientation); whereas, that grasp component is directed towards the intrinsic properties of the target (size, shape). The reach serves to transport the hand to the target using largely proximal musculature and is dependent upon egocentric (body-wise) guidance while the grasp shapes the hand in proportion to the target size for accurate target purchase using largely distal musculature and is dependent upon allocentric (target-wise) guidance.

This theory has received further support from anatomical, physiological, and neuroimaging studies (Culham & Valyear 2006; Vesia et al. 2013; Andersen et al. 2014; Kaas & Stepniewska 2016).

4.4 Discussion

The dual visuomotor channel theory is dependent on the assumption that vision is the only sensory modality that guides prehension. This is a fair assumption as it is under concurrent visual inputs to the dorsomedial reach pathway and dorsolateral grasp pathway that the reach and grasp are completed as a single synchronous act. The role of vision during prehension is highlighted by gaze anchoring of the target from the time of movement onset to about the time the target is grasped (Sacrey & Whishaw 2012b). Visual attention is essential for identifying the reach endpoint and for coordinating hand closure for target purchase. Sensory guidance for the reach-to-grasp movement, however also stems from inputs such as somatosensory and cognitive cues. Such instances occur when reaching without vision and when pantomiming.

Prehension when completed blindfolded, as was done by Karl et al. (2012), dissociates the reach and grasp components. In this study, blindfolded participants were required to reach out and grasp an unknown target (blueberry, round donut, and orange slice) presented to them at random. In performing the task, a common strategy was adopted: participants, likely using proprioception, first reached out with an open hand to establish contact with the target; after contact, the hand shaped appropriately to the target, likely guided by haptics. As vision is essential in accurately guiding the reach and grasp, the removal of vision shifted visions primary role in guiding prehension to other somatosensory processing systems. Not only does this experiment provide an exemplary dissociation of the reach and grasp components, but it is also displays the flexibility of our somatosensory system when coping with unavailable input. Under limited visual feedback conditions, other sources of information are available to guide movement execution. These other sources include proprioception, kinesthetic feedback, and efference copy.

Visual feedback is also reduced in tasks of pantomime, but not all pantomime tasks are equal with respect to the intrinsic (size, shape, colour) and extrinsic (location, orientation) cues available. The literature, as mentioned in the chapter one of this thesis, has a loose definition of what constitutes a pantomime action. Because of this loose definition, studies which compare real and pantomime actions may only be illuminating one piece of the complex neural networks that govern conscious pantomime movement. For this reason, all studies utilizing pantomime can be thought to reside a ‘pantomime continuum’: an alteration in the degree of available intrinsic and/or extrinsic cues.

Experiment 2 of the present thesis, was the first study to directly examine the effects of differing contextual cues on the kinematic and visual behaviour of the reach-to-grasp action by testing three variations of pantomime. The most extreme form of pantomime, though vision was still available, was the complete pantomime condition (Experiment 1 and 2) which required participants to pantomime the reach-to-grasp movement in the absence of the intrinsic and extrinsic cues normally provided by the target and its surface. In performing the task, participants reached out into the general vicinity of the past location of the target and then performed a grasping action signaled by the closing of the digits. The kinematics differed from that of real prehension but were adequate in terms that it was obvious that the participants were conveying a reach-to-grasp movement. Gaze anchoring in this task was also directed in the general vicinity of the movement but did not anchor to the targets past location nor the location of the hand as it made the pretend grasp.

In stark contrast to the study by Karl and colleagues where participants executed the reach-to-grasp movement to a present target while blindfolded the complete pantomime condition required participants execute the reach-to-grasp movement under full vision but the target nor its surface were present. This had a significant effect on the sensory guidance mediating the act. As mentioned above, in Karl's experiment the reach was likely mediated by proprioception and the grasp by haptics, but for the complete pantomime condition of this thesis no haptic feedback is available while general visual cues were. This lead to a simplification in the synchrony of the reach and grasp components likely mediated by stored percepts of the entire movement.

In the complete pantomime condition, neither the reach nor the grasp components in terms of both kinematics and gaze-point data resembled a real reach. This finding is aligned with the current action-perception model proposed by Goodale (1994). The complete pantomime condition abides by this model as the components of prehension are changed and visual attention is indistinct. For these reasons it is likely that the prehensile act is not mediated online with vision, but instead is guided offline by ventral stream pathways.

According to the action-perception theory of prehension, all reaches executed under altered intrinsic/extrinsic cues (pantomimed) should follow the same kinematics and visual attention as observed during the complete pantomime task just described. The findings of this thesis, however, suggest otherwise. On the whole, there is no doubt that the behavioural kinematics of a real reach-to-grasp task and a pantomime reach-to-grasp task, regardless of whether the pantomime action is performed on the transformed or remembered intrinsic/extrinsic cues of the target, are different (Goodale & Milner 1992; Goodale et al. 1994; Westwood et al. 2000; Westwood et al. 2001; Goodale et al. 2005; Cavina-Pratesi et al. 2010b; Pettypiece et al. 2010; Kuntz & Whishaw 2016). What remains at debate is why these differences occur and are they to the same degree regardless of pantomime context. In regards to this question, the 'pantomime continuum' is relevant and plays a large role to the degree of real vs pantomimed action produced and therefore the neural underpinnings of said action. Specifically, it may neutralize the controversy that exists in relation to the dorsal 'action' stream and the ventral 'perception' stream.

Namely, there is a discrepancy in the proposed segregation of the neural networks mediating real and pantomimed actions when comparing studies of different methodological means, i.e. fMRI studies vs. lesion and behavioral studies. It is likely that the discrepancy between studies of different methodological means is not due to the inaccuracy of the method or one method being superior to that of another, but to the difference in how the pantomime task is employed. For example, an fMRI study completed by Króliczak et al. (2007) aimed at comparing the reach and grasp components of prehension, found that within aIPS the difference between reaching and grasping were much stronger for real actions than pantomime. Pantomime reaching for this study consisted of reaching to the surface adjacent to the target with a closed fist, while pantomime grasp consisted of reaching to and shaping the hand for a grasp on the surface adjacent to the target. Because the task conditions always included a surface endpoint to complete the action, whether it be the pantomime reach or pantomime grasp, it is not surprising then that the difference in AIP activation between the pantomime reach and grasp did not reach significance. Further, this study reported that dorsal stream reach regions are active during both real and pantomime prehension. Again, as the surface marking the reach endpoint was physically present, it could be used to execute the reach online mimicking the reach component more accurately while the grasp remained fully pantomimed.

Goodale et al. (1994) performed a series of experiments to observe kinematic differences between real and pantomimed actions, one of which resembles the pantomime task set out by Króliczak: participants executed a reach-to-grasp action on the surface adjacent to the present target. Goodale and colleagues also observed participants in another pantomime condition. In this condition, pariticipants participants reached out and pretended to grasp a target after a delay period (2 and 30 seconds). During all of these pantomime conditions, the kinematics of prehension directed either to the remembered target or adjacent to, differed significantly from those observed for real target directed actions. This series of experiments was crucial in the establishment of the action-perception theory, it however does not provide a comprehensive comparison of the differential effects of altering the intrinsic and extrinsic cues of the task.

The first task in which the pantomime is performed after a brief delay has removed the online acquisition by vision for the intrinsic properties of the target. The extrinsic properties however, are not wholly removed as the surface and allocentric cues to where the target was once located, remain. The second condition in which the target was adjacent to the pretend grasping location has access to more information - in regards to the intrinsic and extrinsic properties. The table surface as well as the adjacent target provide ample information to deduce the extrinsic properties, while the intrinsic properties of the target may be perceived as remaining online with vision, but not with any other sensory processing system. The evidence presented in this thesis, however does not support the conjecture that the intrinsic properties, in the second situation, remain online with vision as gaze point data suggests that the adjacent target is not in foveal vision.

4.5 Caveats

Some caveats must be made with the respect to the current protocol. First, the procedure called for participants to begin with the thumb and forefinger in opposition. Although this permits a common starting aperture and position, it decreases the number of possible kinematic measures. Second, the target for the second experiment was restricted to small food items that could be easily consumed. However, the small size of the skittle brought into question the accuracy of the kinematic measures as the error for the machine and the grasp aperture required to purchase the target were similar. In future experiments, these issues could be resolved by simply using a natural resting hand position at the start and by using larger food items.

4.6 Future Directions

The current thesis as well as other studies involving pantomime reach-to-grasp movements all have some form of external cueing to guide the reach-to-grasp movement. This cueing can be as obvious as the presence of the target and the target's endpoint or as elusive as external room cues. It was clear from the present examination that the target's endpoint plays an important role in accurately guiding the reach by providing a physical anchor point for vision, thus dissociating the reach from the grasp in that participants performed a real reach under visual control but the grasp remained pantomimed. It would then be interesting if the reverse could be accomplished: a pantomime reach with an online grasp. Such a condition may be accomplished by having participants reach in the absence of all cues, such as a dark room, and only have the target illuminate when the hand is within a specific distance. In this scenario, it is likely that the reach will be guided by ventral stream percepts up to the point of target illumination in which an online grasp with pre-shaping could occur.

4.7 Concluding Remarks

Our ability to make complex hand movements is not only reliant on our highly adapted visual system for controlling our movement but can also be guided by higher cognitive functions and other sensory modalities such as proprioception. To that effect, the act of prehension is not as fixed as first purposed by Jeannerod, in actuality it is quite flexible – not relying solely on vision to guide its actions, but when necessary is able to make prehensile movements with similar likeness under the guidance of somatosensation and higher cognitive functions. As we were able to dissociate the reach and grasp components by altering the contextual cues available during a pantomime reach-to-grasp task, it is likely that the reach and grasp components of prehension are independently mediated and can access either more dorsal pathways or ventral pathways based on the contextual cues of the given situation. The neural networks mediating pantomime actions can be simplified by applying a metaphor of mix-and-match: the channels utilized for a single reach-to-grasp action change based on the cues available. In other words, pantomime actions cannot be associated to a single channel any more than they can be classified to a single stream. Pantomime is dependent on a mix-and-match model whereby the intrinsic and extrinsic cues dictate the neural control of the action executed. Under this model, prehension directed to a target will integrate the reach and grasp components into a single seamless act. This likely occurs online with vision using dorsal stream pathways; specifically, via concurrent dorsomedial and dorsolateral channels. A pantomime reach-to-grasp action, on the other hand, where neither the target nor the supporting surface is present is likely mediated by the ventral perceptual stream as both the intrinsic and extrinsic cues that guide the reach and grasp must be derived offline. When prehension is executed to the supporting surface without the target, we see a dissociation in the reach and grasp components. We propose that in this circumstance we first see a reach that is mediated online under visual control to the modified extrinsic properties via the dorsal medial reach channel and the grasp via the ventral stream. Thus, mix-match!

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