THE PARALLEL ENCODING OF ACTIONS WITHIN A SEQUENTIAL GRASPING TASK: STRATEGIC, MOTOR, OR PERCEPTUAL INTERFERENCE EFFECTS

by

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ABSTRACT

Every day we are constantly performing consecutive grasping actions to complete our desired goals. Although we have a good scientific understanding about how the brain programs one grasping action towards a single object, we still have a very limited knowledge about how the brain programs a grasping action within the context of a sequential task. The aim of this dissertation was to investigate whether the characteristics of the second object in a sequence can strategically influence or interfere with how the first object is grasped. Specifically, we explored whether the size and/or the orientation feature of the second object would have any effect on how the grip aperture and grip orientation is selected when performing the first action towards a cylindrical object that varied between two sizes. The task requirement associated with the second object varied across several experiments: participants were either grasping the second object, performing a perceptual judgment about it, or grasping it but with vision occluded. Although the first object was a cylinder that could afford to be grasped with a wide range of grip orientations, the results never revealed that the orientation of the second object had a direct influence on the grip orientation selected to grasp the first object across all experimental manipulations. This also remained true when only strictly manipulating orientation (no size manipulation). However, when the second object was smaller than the first object, we found a consistent pattern of results where participants reached out with a smaller peak grip aperture relative to when the second object was the same size or larger. Based on these results, it is suggested that the second object within a sequential task will only interfere with the grasping kinematics towards the first object when both action plans have overlapping features, and most importantly this is not dependent on providing a strategic benefit to the overall movement. It is speculated that this specific pattern of results is due to a motor interference effect driven by the parallel encoding of grasping actions within the anterior intraparietal area (i.e., the grasping circuit).

LIST OF ABBREVIATIONS AND SYMBOLS USED

ANOVA	Analysis of variance
fMRI	Functional magnetic resonance imaging
η_p^2	Partial eta squared
PGA	Peak grip aperture
RT	Reaction time
MT	Movement time
V1	Primary visual cortex
M1	Primary motor cortex
PMd	Dorsal premotor cortex
PMv	Ventral premotor cortex
AIP	Anterior intraparietal area
SPOC	Superior parieto-occipital cortex
MIP	Medial intraparietal sulcus
SMA	Supplementary motor area
pAF	Posterior segment of the arcuate fasciculus
vOF	vertical occipital fasciculus
TMS	Transcranial magnetic stimulation
EMG	Electromyography
ID	Index of difficulty
LCD	Liquid Crystal Display
M	Mean
SE	Standard error

SEM	Standard error of the mean
Hz	Hertz
MS	Milliseconds
MM	Millimeters
α	Alpha
IRED	InfraRed emitting diode
TEC	Theory of event coding
° or Deg	Degrees
ST	Simultaneous tilt
RF	Rod-and-frame

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CHAPTER 1: INTRODUCTION

1.1 Purpose

Before you start to read the fascinating science presented within this dissertation, think back of the last activity you did prior to opening this document…

Whether it was something as simple as making a pot of coffee or something as complex as building a shelf from Ikea, multiple sequential grasping actions needed to be executed and coordinated to successfully complete the task. In fact, most of our activities of daily living rely on combining multiple successive actions that require us to reach towards, grasp, lift and transport objects within a continuous sequence. Although our nervous system performs these actions effortlessly daily, our understating of the neural computations involved in the planning, programming, and execution of sequential grasping actions is surprisingly very limited.

Within the last four decades there has been immense scientific progress towards understanding the neuroscience of grasping (as highlighted by reviews from Castiello, 2005, Castiello & Begliomoni, 2008, Grafton, 2010, Turella & Lingnua, 2014). Specifically, building on Ungerleider and Mishkin's research (1982), Milner and Goodale (1992) provided us with the influential dual-stream theory of visual processing which identified separate, but interacting, neural networks for the perception of objects (ventral stream network) and the visual control of actions (dorsal stream network). Since then, there have been a plethora of research dedicated to understanding the function of each stream (see section 1.3 for more details) which led to major discoveries about the specifics on how the brain programs a grasping action. However, a major caveat about these discoveries is the fact they were found by using research paradigms where participants are simply required to reach out and perform one single grasping action to one single target object.

This is not only problematic in terms of an attention standpoint, since we rarely encounter one single object in our environment – for example, as I am picking up my coffee mug from my desk there are many other objects surrounding my caffeinated target - but also problematic in terms of "real life" action planning. As I made you realize in the opening paragraph, we accomplish most of our daily tasks by performing multiple sequential actions in the presence of multiple objects. This implies that our brain potentially plans multiple actions towards multiple objects even prior to initiating the very first movement of the action sequence. Although the literature on the visual control of grasping has provided us with a very good understanding about how the dorsal visual stream network operates as a non-conscious online processor when controlling a single action towards a single target (Desmurget et al., 1999; Pisella et al., 2000), there are many reasons to assume that planning a multi-segment action (e.g. two consecutive grasping actions) will require more complexity in motor programming and the additional involvement/recruitment of other cognitive processes (i.e., attention and memory factors associated with planning more than one action).

A classic motor behaviour study by Henry and Rogers (1960) was one of the first studies to experimentally demonstrate differences between the planning of single-segment movements relative to multiple-segment movements. Specifically, they showed that participants' reaction time (RT) to initiate the first movement of a sequence was directly related to the complexity of the sequence (e.g., a sequence that required more actions increased the RT for the first movement relative to a sequence that required less actions - even though the first movement was the exact same for each sequence). The results of this study revolutionized our understanding of motor programming and triggered a paradigm shift for how movement researchers conceptualized information processing (Fischman et al., 2008). Since then, studies have confirmed that multiple-segment movements require more complex planning (increase in RT) and online control processing (increase in movement time to complete first movement segment) than single-segment movements (i.e., the one-target advantage: Adam et al., 2000; Chamberlin & Magill, 1989; Fischman & Reeve, 1992). The leading explanation (see section 1.6 for more details and other possible explanations) for the one-target advantage phenomenon is due to the interference of preplanning the second movement while the first movement is being executed (i.e., movement integration hypothesis: Adam et al., 2000; Bested et al., 2018). However, the great majority of evidence supporting the movement integration hypothesis used a sequential pointing task and did not explore sequential grasping actions. Since the neural substrates for controlling the hand trajectory (e.g., pointing at a target) are different than the substrates controlling the shaping of the hand (Kurata, 1993; Rizzolatti & Luppino, 2001; Davare et al., 2006), it essential to further explore if this theory holds true when performing sequential grasping actions.

Based on the current state of the literature, we know a lot about performing one single grasping action and performing successive pointing actions, yet we have very limited knowledge of what happens when we perform sequential grasping actions. To complicate things even further, the main theories leading both research programs are contradictory to each other. Within the grasping literature, evidence shows that the shaping of the hand when performing a grasping action is very resistant to interferences since this process is controlled outside of our conscious awareness (i.e., hand shaping not fooled by visual size illusions: Agiloti et al., 1995, Haffenden et al., 2001; Westwood & Goodale 2003). Whereas evidence from the sequential pointing literature shows that the initial action of a sequence is heavily interfered by the future action(s). Therefore, the goal of the experiments presented within this dissertation seeks to provide further understanding of how the brain plans, programs and executes sequential grasping actions by specifically exploring if/how the features of the second object in a sequence influence the shaping of the hand towards the first object.

Although limited, there is research that has already explored this question and the evidence suggests that the characteristics of the second object in a sequence can indeed directly influence the grasping action towards the first object (Hesse & Deubel, 2010; LeBlanc & Westwood, 2016; Seegelke et al., 2012, 2013, 2015). However, the exact mechanism of how and why this happens remains disturbingly ambiguous. It is for this reason that the aim of this dissertation is to provide clarity on what specific characteristics of the second object can interfere with the first grasping action (e.g., orientation vs. size) and why does it happen (e.g., action efficiency, motor interference, or perceptual interference). To clearly articulate the logic behind each research question and to properly present the evidence gathered from this dissertation, it is important to firstly provide a brief overview of the main research areas of interest. This includes breaking down the grasping kinematic measures of interest, the two cortical visual systems, the neural correlates of grasping, the role of attention in action selection, and the planning of sequential actions.

1.2 Grasping Kinematics

When planning to interact with an object, the type of action executed is not only determined by the object's visual properties but also by the intended activity to be performed (Napier, 1960). For example, if a fresh hot cup of latte is sitting on the counter and your intention is to drink it, you will reach out with your thumb and index finger to precisely grip the little handle on the side of the cup. In contrast, if your intention is to move the cup out of your way, you will reach out and grasp the top of the cup with all fingers to simply move and place the cup at another location. This example demonstrates that the same object can afford to be grasped and manipulated in multiple ways depending on the end-goal, as shown experimentally (Ansuini et al., 2008, Cohen & Rosenbaum, 2004, Armbrüster & Spijkers, 2006). Thus, the goal of the action will drive the type of grasp that will be programmed and deployed towards the object. However, how does the brain coordinate and control the biomechanical complexities of shaping the hand into a specific grasp posture to successfully interact with the objects in the environment?

The scientific study of grasping was significantly advanced by Napier's influential studies (1956, 1960, 1993) which explained the functional duality of the primate hand for performing grasping actions. Napier described and documented that the hand can utilize two general grip forms to interact with objects in the environment: the power grip (i.e., all fingers press down on an object with the thumb making counter pressure) and the precision grip (i.e., index finger and thumb press down on each end of the object). The power grip serves to grasp an object with high force and stability by flexing all fingers around the object, whereas the precision grip serves to precisely manipulate objects by controlling the tips of the thumb and index finger.

Unlike the power grip, the precision grip requires the fine control of independent finger movements (directions and force magnitudes) to match the object's shape with the desired amount of force (Ansuini et al., 2006, Flanagan et al., 1999, Johansson, 1996, Zatsiorsky & Latash, 2008). As a result, the control of fingertip actions with a precision grip engages neural circuits that are different than the power grip action (Ehrsson et al., 2000) regardless of the size of the target object (Begliomini et al., 2007). It has been shown that subpopulations of neurons in the primary motor cortex (M1) that project to motor neurons that activate hand muscles are active while conducting a precision grip but not during a power grip, even though the same target muscles are activated in either grasp (Muir & Lemon, 1983). In addition, neurons in the anterior intraparietal sulcus (AIP) will respond differently to a single object depending on whether it must be grasped with a power grip or a precision grip (Baumann et al., 2009), and the activity of neurons in the ventral premotor area (PMv) are determined by the specific type of grip and posture used to grasp the object (Murata et al., 1997, Roas et al., 2006, Rizzolatti et al., 1988). Therefore, because the type of grasp to be deployed will trigger a different cascade of neural events to successfully execute the desired action, it is important that I explicitly state that the series of experiments presented within this dissertation will be strictly measuring and analyzing the kinematics from grasping with a precision grip. So, each time the term grasping is used within the following text it will specifically refer to the precision grip unless otherwise noted.

The act of reaching out and grasping an object can be broken down into three distinct components (Jakobson & Goodale, 1991): the reaching component (extending your arm towards the spatial location of the object), the grip formation component (scaling the opening of the thumb and index finger in accordance with the geometrical properties of the object), and the object manipulation component (grasping and lifting the object). The initial phase of transporting the hand towards the object is performed in fast-velocity, whereas the final transport phase of closing the fingers and forming a grip onto the object is performed in low-velocity (Jeannerod, 1984). The low-velocity phase consistently begins at about 75% of the movement time (Jeannerod, 1986). In addition, looking more closely at the anticipatory posturing of the thumb and index finger (grip formation component), there is first a progressive opening of the grip, with straightening of the fingers followed by a gradual closure of the grip until it matches the object's size. Within 60-70% of the movement duration is the point of time at which the opening of the thumb and index finger is the largest. This identifiable landmark of the movement is known as peak grip aperture (also commonly referred to as maximum grip aperture), which is highly correlated with the size of the target object (Jakobson & Goodale, 1991).

Since peak grip aperture (PGA) happens during the initial fast-velocity phase of the movement, this demonstrates that our hand already begins to reflect the size of the target object as soon as the reach-to-grasp movement is initiated (Jackobson & Goodale, 1991, Jeannerod 1984, Jeannerod et al., 1995). The same applies for the orientation of the hand. The angle of the grip formation during the initial fast-velocity phase already matches the orientation of the object (Cuijpers et al., 2004, Glover & Dixon, 2011; Mamassian,1997). The fact that our grasping hand reflects the features of the target object (e.g., size and orientation) as soon the movement is initiated suggests that the preparation of a grasping action must heavily rely on the visual processing of the object. However, does the visual control of action rely on the same visual processing mechanisms that we use for consciously perceiving and recognizing objects in our environment?

1.3 The Two Visual Systems

Before diving into the details of how visual information is utilized to properly program the motor coordination of a grasping action, it is first important to highlight that our visual system is not a unitary system. In the late 1960s, research from Trevarthen (1968) and Schneider (1969) proposed the visual system served two distinct functions based on the different retinal projection pathways. Specifically, their evidence suggested that the tectopulvinar system (retinal projections to the superior colliculus) provided the function of stimulus localization and the geniculostriate system (retinal projections to the lateral geniculate nucleus) served the function of stimulus identification. Although it would be shown that not all behaviour associated with localizing a stimulus depends on the activity of the superior colliculus (Ingle, 1973, 1980; Ellard & Goodale, 1998), the proposal that our visual system could be organized into two functionally distinct system (vision for target identification vs. vision for target localization) was further explored.

In 1982, Ungerleider and Mishkin gathered electrophysiological, anatomical, and behavioural evidence suggesting that the processing of visual information was mediated by two divergent neural pathways that originate from the striate cortex. The ventral stream projections that reach the inferotemporal cortex control the processes responsible for object recognition and the dorsal stream that projects to the posterior parietal cortex is responsible for spatial vision. The most convincing evidence supporting this claim was the fact that monkeys with lesions of the inferotemporal cortex could not successfully complete visual discrimination tasks, but their performance was not affected when completing visuospatial tasks (Gross, 1973); whereas the opposite results were shown for monkeys with lesions of the posterior parietal cortex (Pohl, 1973, Ungerleider & Brody, 1977, Milner, Ockleford, & Dewar, 1977). This view of how vision is organized at the cortical level became referred to as the *what* and *where* pathways, since the ventral stream serves to provide the visual input for perception of object recognition ("what" is the object) and the dorsal stream serves to provide the visual input for perception of spatial relationships among objects ("where" is the object).

As evidence grew in favour of Ungerleider and Mishkin's (1982) two cortical visual systems hypothesis (Boussaoud, Ungerleider, & Desimone, 1990), the concept of two separate visual systems got further refined by research demonstrating that the type of information that feeds into the ventral and dorsal streams of the striate cortex are supplied by two distinct channels relative to the subdivisions of different retinal ganglion cells (Livingstone & Hubel, 1988). Specifically, different types of ganglion cells (P cells and M cells) synapse on different layers (parvocellular and magnocellular layers) of the lateral geniculate nucleus (LGNd) thus creating two distinct channels of information projecting out to the levels of the striate cortex. As a result, Livingstone and Hubel (1988) proposed that the flow of information to the ventral stream was fed by the parvo channel – a channel dedicated to gathering the required visual information for object identification (form and colour properties); and the dorsal stream was fed by the magno channel – a channel that supplies visual information for the purpose of locating objects in space (depth and motion properties). Although this converging evidence provided a unified framework to conceptualize the hierarchical processing of the 'two visual systems' hypothesis, it would later be shown that the parvo and magno inputs in the striate cortex were not as distinct as initially described (Maunsell, Nealey, & DePriest, 1990; Nealey & Maunsell, 1994). In addition, newly gathered neuropsychological evidence suggested the dorsal stream provides a crucial function for the visual control of action (Perenin & Vighetto, 1988; Milner et al., 1991; Goodale et al., 1991) – a function not accounted for by Ungerleider and Mishkin's (1982) two cortical visual system model[1].

Patients with lesions in the superior regions of the posterior parietal cortex (dorsal stream) will show difficulties in correctly producing grasping and aiming movements towards a target object despite the fact they can correctly describe the orientation and position of the object (Prenin & Vighetto, 1988). In contrast, a patient with damage localised to the lateral occipital area of the ventral stream is unable to indicate the size, shape, and orientation of objects but shows no impairment when reaching out and grasping the object (Milner et al., 1991; Goodale et al., 1991). This led Goodale and Milner (1992) to propose a new explanation for the function of the dorsal and ventral streams. Unlike Ungerleider and Mishkin's (1982) model that was based on the premise that the function of each stream was driven by input distinctions (object location vs. object qualities), they proposed that the segregation of the streams is to serve different output requirements in which the ventral stream serves the function of visual perception (vision-for-

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[1] They would later modify their model to include visuomotor control as a function of the dorsal stream (Boussaoud, Ungerleider, & Desimone, 1990; Haxby et al., 1993).

perception), and the dorsal stream serves the function of visuomotor control (vision-for-action). According to the Goodale and Milner's perception-action model, the dorsal stream which was previously considered the *where* pathway is now conceptualized as the *how* ("how" to interact with the object) pathway: a stream responsible for the visual control of goal-directed movements (e.g., reaching towards the correct location and correctly shaping the hand to properly interact with a target object).

Therefore, each stream will process information relating to the structure of objects and their spatial locations, but each stream will transform this information into different functional outputs (Goodale & Milner, 1992; Goodale & Humphrey; 1998; James et al., 2002; Ganel & Goodale, 2003). The ventral stream will compute the output leading to the identification and recognition of objects (e.g., conscious perception: recognizing the coffee mug) while the dorsal stream will compute the necessary output required to effectively interact with the object (e.g., visual control of action: reaching out and grasping the coffee mug). The perception-action model view of the visual systems (Goodale & Milner, 1992) further reinforced the concept that there is no single representation of space ('spatial perception') in the brain but instead each stream utilizes a different spatial coding system to achieve its function. The dorsal stream will utilize an egocentric (self-to-object frame of reference) spatial coding system for the control of action, and there are multiple effector specific coordinate systems within the dorsal stream (Rizzolatti et al., 1994; Cohen & Andersen, 2002; Henriques et al., 2002). Whereas the ventral stream operates with an allocentric (object-to-object or scene-based frame of reference) coding system for perceiving the spatial relationship of an object among other objects (Goodale & Humphrey, 1998). Essentially, the ventral stream utilizes an allocentric and holistic approach when producing vision-for-perception (e.g., background information influences how we perceive and recognize a target object) whereas the dorsal stream utilizes an egocentric and analytical approach (e.g., only codes for the absolute metrics of the target object independent of its surrounding background information) when producing vision-for-action (Ganel & Goodale, 2003).

Goodale and Milner's theoretical framework for the perception-action model was ignited by the performance observed in patient D.F. who had lesions in the lateral occipital area of each hemisphere (Milner et al., 1991; James et al., 2003). The location of the brain damage caused D.F. to have profound visual form agnosia in which she is unable to perceive/recognize objects. However, D.F. can successfully post a wooden card into a series of slots placed at different orientation (visuomotor task) despite the fact she fails to match the orientation of the slots with the wooden card when performing the task as a perceptual matching task (Goodale et al., 1991). This demonstrates that D.F. can use visual information for the visual control of action (dorsal stream process) but cannot use visual information for recognizing objects (ventral stream process). Furthermore, D.F. is not only unable to identify a target object but is also unable to manually estimate the size of the object (mime its width using finger and thumb). However, when asked to reach out a grasp the object, she reaches towards the correct location while correctly scaling her grip formation to the correct size (Goodale et al., 1991; Goodale & Milner, 1992). In contrast, patient R.V. who has bilateral lesions of the occipitoparietal cortex (dorsal stream) can describe the target object and can correctly estimate the size of the object via manual estimation but fails to properly calibrate the size of the aperture between her thumb and index finger when reaching out to grasp the object (Goodale et al., 1994). Similar evidence also showed strong support for this double dissociation in which perceptual impairments associated with ventral stream damage did not impair visuomotor performance (Carey et al., 1996; Goodale et al., 1991; Goodale et al., 1994) while visuomotor impairments associated with dorsal stream damage did not impair perceptual performance (Binkofski et al., 1998; Jakobson et al., 1991; Jeannerod, 1986; Jeannerod et al., 1994); and later evidence would further confirm and refine the function of each stream and its neural correlates via the use of functional magnetic resonance imaging (fMRI) techniques (Culham et al., 2003; Fang & He, 2005; James et al., 2003; Valyear et al., 2006).

Furthermore, psychophysical studies using healthy participants have also shown results in support of the perception-action model of vision. Specifically, using the Ebbinghaus size-contrast illusion, Aglioti, DeSouza, and Goodale (1995) revealed that participants misjudged the size of the target stimulus when asked to perform a perceptual judgment – in other words the ventral stream process was being 'fooled' by the illusion. However, when instructed to reach out and grasp the same target stimulus, participants were accurately scaling the size of their grip aperture – in other words the dorsal stream process was NOT being 'fooled' by the illusion. Many other studies reported similar findings using different types of illusions (Ganel, Tanzer, & Goodale, 2008; Haffenden & Goodale, 1998; Haffenden, Schiff, & Goodale, 2001; Hu and Goodale, 2000; Whitwell et al., 2018; Westwood, Heath, & Roy, 2000). This line of evidence, although controversial (Franz et al., 2000; Franz, 2003; Franz & Gegenfurtner, 2008; Kopiske et al., 2016 Pavani et al., 1999; Vishton et al., 1999), allowed researchers to develop novel methods to explore and refine the perception-action hypothesis and its mappings on the brain.

Specifically, Dyde and Milner (2002, 2003) showed that participant's hand orientation when grasping a target embedded within a simultaneous tilt (ST) illusion was affected by the illusion, but hand orientation was not affected when grasping a target embedded within a rod-and-frame (RF) illusion. Since the effect of the ST illusion is due to processing happening 'early' at the level of the striate cortex, it can affect the action deployed towards the illusion since the dorsal stream will carryover this information when planning the action. However, since the effect of the RF illusion is due to processing happening ‘later’ in the inferotemporal cortex in does not affect the action since dorsal stream does not need to access to this type of processing to properly plan out and execute the action. However, when programming these actions based on memory (no vision), the dorsal stream heavily relies on this ventral stream process to program the desired action (Cohen, et al., 2009; Gentilluci et al., 1996, Hu & Goodale, 2000; Rossetti, 1998, Westwood et al., 2000).

Using a size-contrast illusion, Westwood and Goodale (2003), as predicted, showed that when a target is visible between the response cue and the movement onset, the size-contrast illusion does not affect participant’s peak grip aperture (PGA) when reaching out to grasp the target. In contrast, when the target is occluded from view directly prior to movement onset, the illusion does affect PGA (e.g., PGA was larger when the companion object was smaller than the target object since the target object perceptually appears bigger next to the smaller object – classic size contrast illusion effect seen with measurements of perception). The fact that the illusion persisted in affecting participant’s grip scaling towards the object even though participants could see the target right up until movement onset strongly suggested that the dorsal stream operates in real-time and needs the target to be visible to optimize its computational function. In addition, it also suggested that when the target object is not directly visible, the control of action will recruit networks from the ventral stream to access the perceptual representation of the object to guide action, hence why memory-driven actions are more susceptible to perceptual illusions (Goodale et al., 2004; Gentilluci et al., 1996, Hu & Goodale, 2000; Singhal et al., 2003; Westwood et al., 2000; Westwood et al., 2001; Westwood & Goodale, 2003).

Nevertheless, when operating under full visual control, the dorsal stream will act as an ‘automatic pilot’ that operates outside of our conscious awareness (Pisella et al., 2000). Specifically, the hand trajectory will correct its path while reaching out for targets that jumped position even though participants were not consciously aware that the targets shifted locations and the participants could also not see their hand in action (Goodale et al., 1986; Prablanc & Martin, 1992). This type of evidence implies that the dorsal stream is computing error signals generated by comparing the desired action (internal model) to its real-time motor outflow (forward model) thus allowing for real-time feedback control (Clower et al., 1996; Wolpert et al., 1995, 1998). Specifically, applying transcranial magnetic stimulation (TMS) to the posterior parietal cortex at movement onset disrupted the stereotypical hand path corrections that occur when participants reached towards targets that jumped location, but it did not affect actions towards targets that remained stationary (Desmerget et al., 1999). This ‘online control’ corrective process is one of the hallmarks of the dorsal stream and this process acts independently from the ventral stream’s conscious visual processing (Pisella et al., 2000).

Based on the overwhelming evidence supporting the two visual systems hypothesis (for latest review see Goodale and Milner, 2018), it is now evident that the brain areas responsible for the visual control of action differ from the brain areas that give rise to our conscious visual perception. Since the research in this dissertation will investigate measurements of planning a grasping action, it is important that we now further investigate the specific networks within the dorsal stream that specifically allows us to transform the intrinsic properties of an object into the appropriate motor output: correctly scaling the aperture and orientation of our fingers when reaching out to grasp the object.

1.4 The Neural Correlates of Grasping

Even prior to Goodale and Milner’s (1992) revolutionary proposal about the function of the dorsal stream, it was well established that the primary motor cortex (M1) and its descending projections to the spinal cord (specifically the corticospinal tract) are responsible for activating the appropriate set of muscles to generate the desired movement of the fingers for executing a goal-directed grasping action (Denny-Brown, 1950; Muakkassa & Strick, 1979; Godschalk et al, 1984, Lassek, 1954; Lawrence & Hopkins, 1976 and Matelli et al., 1986). In addition, the cerebellum and basal ganglia also play crucial roles in maintaining control and coordination when performing a grasping action (Smith and Bourbonnais, 1981; Smith et al., 1993; Gibson et al., 1994; Wenger et al., 1999;). However, to trigger the execution of the action (the role of M1), the intrinsic properties (size and orientation) of the target object must be first processed visually to trigger the correct type of action (Jeannerod et al., 1995). Converging evidence from monkey neurophysiological and human neuroimaging studies revealed a network within the dorsal stream responsible for the preshaping of the hand in accordance with the object’s intrinsic properties (Brochier & Umiltà, 2007; Castiello & Begliomini, 2008; Culham et al., 2003; Culham & Valyear, 2006; Fagg & Arbib, 1998; Jeannerod et al., 1995; Rizzolatti & Luppino, 2001; Rizzolatti & Matelli, 2003).

Specifically, from the striate cortex the dorsal stream can be further subdivided into two distinct, yet very interactive (Grol et la., 2007; Takahashi et al., 2017; Turella & Lingnau, 2014), pathways. The dorsomedial pathway consists of connections forming from the superior parietal occipital cortex (SPOC) and the medial intraparietal sulcus (MIP) with the dorsal premotor cortex (PMd; Bosco et al., 2010; Caminiti et al., 1991; Filimon et al., 2009; Johnson et al., 1996;

Prado et la., 2005). This pathway specifically codes for reach related information for the planning and control of action during the transport phase (e.g., directing the arm and hand towards the object's location; Rizzolatti et al., 1998). However, the dorsolateral pathway is formed by connections between the anterior intraparietal sulcus (AIP) and the ventral premotor cortex (PMv) and this pathway is specifically involved in transforming the intrinsic properties of the target object into the desired motor output (e.g., scaling of the hand's aperture and orientation; Binkofski et al., 1998; Culham et al., 2003, 2006; Filmon, 2010; Fluet et al., 2010; Frey et al., 2005; Murata et al., 1997; Raos et al., 2006; Rizzolatti et al., 1988).

Specifically, monkey neurophysiological studies have shown that many of the neurons in PMv are selective visuomotor neurons in which each action is represented by specific different subpopulations of neurons; coded by different classes of action: grasping vs. tearing, specific types of action: precision grip vs. power grip, and the temporal aspects of the action: opening the fingers vs. closing the fingers (Murata et al., 1997; Rizzolatti et al., 1988). The fact that a selective PMv visuomotor neuron will discharge when planning an action towards an object but also when simply viewing the same object (or one that affords a similar action) suggests that PMv might automatically code a 'potential action' for the observed stimulus (Rizzolatti & Luppino, 2001).

PMv also receives a major input from the AIP (Luppino et al., 1999) and this area contains more 'diverse' neurons. Sakata et al. (1995) classified three main classes of neurons in the AIP. The 'motor-dominant' neurons will fire during grasping performed in both light and dark (no vision), but they do not discharge during object fixation. The 'visual-dominant' neurons discharge during grasping in light and when fixating the object but they remain silent during grasping in the dark. The 'visual and motor' neurons will fire more strongly when grasping in light relative to dark and they also fire during object fixation. The fact that these neurons show a greater response during grasping in light strongly suggest that vision of the object potentiates the motor response. Furthermore, since the ‘visual dominant’ neurons will selectivity respond to the presentation of one type of object among a large variety of other objects, this indicates that there are populations of neurons in the AIP dedicated in coding the visual information about the object’s 3D features (e.g., orientation-selective neurons and size-selective neurons; Murata et al., 2000).

Thus, based on a proposed model of the visuomotor grasping circuit (Fagg & Arbib, 1998; Rizzolatti & Luppino, 2001), the ‘visual dominant’ neurons of the AIP are responsible for extracting the object features and initiating the transformation process of object representation into the appropriate motor output (commonly referred to as the motor prototype). More specifically, ‘visual dominant’ neurons will compute the extraction of the 3D features of the object and send the relevant information to ‘visual and motor’ neurons (e.g., action specific feature selection) and its associated ‘motor dominant’ neurons (e.g., grip selection). This information (object/action description) is then shared with the visuomotor neurons of the PMv which will recruit other purely ‘motor’ neurons that will program possible appropriate motor prototypes. The most appropriate motor prototype is then only selected when signaled from the supplementary motor cortex (SMA) – carrying over information from the dorsolateral prefrontal cortex (goals and object meaning) - which will also temporally segment the action and send the associated plan to M1 to execute the motor commands. During this process, the neurons activated within PMv will keep the congruent ‘visual and motor’ neurons of the AIP active during the development of the action, suggesting that the representation of the object remains active throughout the entire action (Murata et al., 1996). The feedback loop between PMv (coding motor aspects) and AIP (coding object's intrinsic properties) also allows the brain to compute any mismatch between the grasp plan (aperture size, orientation of the hand) and the object's properties in real-time (Raos et al., 2006) – the mechanism responsible for the 'online control' feature of the dorsal stream.

The importance of the dorsolateral pathway for performing a grasping action becomes very evident when looking at studies using transient inactivation techniques in which inactivation of either AIP or PMv significantly impaired hand shaping in monkeys when reaching to grasp an object (Fogassi et al., 2001; Gallese et al.,1994). The important role of PMv and AIP for grasping control has also been confirmed in humans with TMS studies that targeted each area and reported similar deficits in coding grasp-related information (Oliver et al., 2007). More specifically, TMS studies have shown the causal role AIP plays in pre-shaping the hand (Davare et al., 2007; Rice et al., 2006; Vesia et al., 2013) and providing online control when faced with object perturbation (Tunik et al., 2005; Rice at al., 2006). It has also been demonstrated that grasping small objects led to an increase in the effective connectivity between PMv and AIP relative to grasping large objects (Grol et al., 2007). Since grasping small objects will require more precise fine movements, this further supports the view that the connections between PMv and AIP specifically play a crucial role in providing the online control needed to accurately execute a precision grasp.

The computations provided by the PMv and AIP circuitry is the driving force responsible for the behavioural effects (or lack of effects) seen in the studies presented in the last section that looked at grasping in the context of the dorsal/ventral visual stream dissociation – grasping does not rely on conscious perception (Goodale and Milner, 1992), grasping not affected by visual illusions (Agiloti et al., 1995, Haffenden et al., 2000), and grasping is optimized when performed under full vision relative to no vision (Westwood & Goodale, 2003). Based on the evidence presented thus far, it seems like if the target object remains in full sight throughout the execution of the action, the grasping hand will accurately scale the opening of its fingers and orientation during the early phase of the action since there is a dedicated network responsible for this crucial function within the dorsal stream. However, the studies discussed within this section and the last section all used paradigms that consisted of performing one action to one single object. This is an excellent way to increase the amount of experimental control to properly investigate which areas of the brain are responsible for controlling/producing a grasping action, but this greatly differs to how we would select and plan actions during our regular daily activities.

Specifically, when performing a goal-directed grasping action there are multiple actions that can be performed to one object, there is typically other objects next to the target object, and oftentimes the goal-directed action will consist of a series of continuous sequential actions involving multiple objects. Thus, it is crucial to investigate how the grasping circuit of the dorsolateral pathway operates when 'bombarded' by other objects and other possible actions. Although the research demonstrated within this section thus far highlighted the functional role of the grasping circuit for effectively executing a single grasping action (pre-shaping the hand & online control) towards one single object, it is now important to investigate how the grasping circuit deals with selecting an action among other possible actions.

When preparing a grasping action, the AIP will be active prior to PMv (Fagg & Arbib, 1998; Castiello, 2005; Jeannerod et al, 1995; Taira et al., 1990). So, if the grasping circuit plays a role in selecting a specific action (and not just providing the computation for its execution), it will mostly likely be a process that is happening within AIP. Baumann et al (2009) used a delayed grasping task, in which monkeys were cued to grasp a handle at one of five different orientations using either a precision or a power grasp to explore to what extent the AIP encodes context-specific information for grasping. When the handle orientation was presented before the grip type was cued, it was shown that the subset of neurons responsible for encoding a power grip and the subset of neurons coding for precision grip were simultaneously activated. However, once the grip type was cued, the subset of neurons for the other grip type decreased its firing while the activity for the subset of neurons of the cued grip type remained active.

As highlighted by Gallivan and Wood (2009), the results by Baumann et al. (2009) shows that the mere presentation of an object can simultaneously activate multiple potential grasping prototypes within AIP. This evidence is consistent with previous research that showed via single-unit recordings that when a monkey is presented with two possible reaching targets, a subset of neurons in the PMd simultaneously encodes the actions for both possible locations till one is cued (Cisek & Kalaska, 2005) and this is specifically driven by the motor, not visual, encoding mechanisms of the potential targets (Gallivan et al., 2017). Similar findings have also been reported in the superior colliculus when planning saccades towards multiple potential targets (Basso & Wurtz, 1997). Thus, the evidence suggests that each effector-specific area within the motor system will encode ‘competing actions’ in parallel till one of them is selected to be executed (Cisek, 2007). However, it is also important to note that the Baumann et al. (2009) results are unique from the other studies since multiple actions were elicited by one single target at one single location. Since grasping can take shape in many different forms (Macfarlane & Graziano, 2009), it seems the AIP will process the possible types of grasping actions in parallel till one is triggered to be executed - even when only one object is present. It is assumed that the properties of the associated neurons in PMv will show similar firing patterns since most of the output from AIP funnels directly into PMv (Luppino et al., 1999). In addition, this assumption conveniently converges with the fact that selective PMv neurons that represent a grasping action will discharge by simply seeing (no action performed) an object that affords that type of grasp; the automatic encoding of action prior to action selection (Rizzolatti & Luppino, 2001).

This evidence shows that the grasping circuit not only specializes in guiding the execution of the grasping action but can also hold multiple action prototypes simultaneously during the planning phase of the action. Before I start to explore how (or if) the representation of multiple actions could potentially interfere with the online control properties of the dorsolateral pathway, which is something that would have not been detected in the previous studies where only one specific action is planned towards one object, it is first important to also highlight that the grasping circuit is not isolated from other areas outside of the dorsal stream.

Specifically, monkey anatomical studies have shown that AIP has strong connections with the prefrontal cortex (Petrides & Pandya, 1984) and AIP also receives direct input from the inferotemporal cortex of the ventral visual stream (Borra et al., 2008; Webster et al., 1994). Similarly, white matter tracts have been found in humans between the superior/middle temporal areas (ventral stream) and the inferior parietal regions (dorsal stream) – the posterior segment of the arcuate fasciculus (pAF; Budisavljevic et al., 2015; Catani et al., 2007) and between the dorsal and ventral areas of the striate cortex – the vertical occipital fasciculus (VOF; Takemura et al., 2016; Yeatman et al., 2013, 2014).

Despite the distinct neuroanatomical and functional properties of the ventral and dorsal visual streams, they are not totally disconnected from each other since the two streams will closely interact when performing complex skilled hand actions (Cloutman, 2013; De Haan & Cowey, 2011; Goodale, 2014; Milner, 2017; Gallivan et al., 2016, Schenk & McIntosh, 2009; van Polanen & Davare, 2015). More specifically, the VOF is strongly involved when reaching to grasp an object and the pAF is strongly involved when lifting the object, but neither VOF nor pAF is strongly involved when reaching for objects (Budisavljevic et al., 2018). Based on these results, it is suggested that the VOF will facilitate the transfer of information from ventral stream regarding the object's form, colour, identity/function, and past experiences with the object (Cohen et al., 2000; Malach et al., 1995; McKeefry & Zeki, 1997; Wade et al., 2022) into the dorsal stream to fine tune the opening of the hand to reduce movement errors when reaching out to grasp the object. As seen in the previous section, this cross-communication becomes very relevant when performing memory-guided grasping actions in which the dorsal stream will rely on the perceptual memory of what the object looks like to guide the action (Cohen, et al., 2009; Gentilluci et al., 1996, Hu & Goodale, 2000; Rossetti, 1998; Singhal et al., 2013; Westwood et al., 2000; Westwood & Goodale, 2003). However, this inter-stream interaction also plays a crucial role when grasping (under full visual control) many of the objects we interact with daily, for example the semantic knowledge of a tool's function (ventral stream process) will directly affect how you reach out to grasp it (Carey et al., 1996; Creem & Proffitt, 2001). In addition, the pAF will provide the information about the object's weight (a property that cannot be coded directly from vision) from the ventral stream (object identity, object texture, past memories of using the object, etc.) to incorporate it into the motor plan to produce the necessary grip and lift fingertip forces (Baugh et al., 2012; Buckingham et al., 2009; Flanagan et al., 2000, 2008; Gallivan et al., 2014; Johansson & Flanagan, 2009; Kentridge, 2014).

Despite the large amount of research demonstrating the distinct functional properties of the dorsal and ventral stream, the two streams will frequently work in collaboration when producing goal-directed grasping actions. Based on the neural organization of the grasping circuit, it makes it possible that when the grasping circuit is faced with multiple objects in sight and multiple possible (current and future) actions, its computational power of correctly scaling the hand and optimizing its online control mechanism might be suboptimal via interferences happening within the circuit (caused by the parallel processing of other action prototypes) or via interferences happening from outside the circuit (caused by perceptual/memory/semantic information from ventral stream connections). Therefore, it is now necessary to examine how the motor system operates when faced with multiple objects and whether the distractors (the non-target objects) can interfere with the action kinematics of the goal directed action.

1.5 The Role of Visual Attention for Action Selection

As elaborated in the previous section, performing a grasping action strongly relies on the visual processing of the object's intrinsic features in which a specialized circuit within the dorsal stream will utilize the visual information for programing the required computations to precisely control the shaping (and online adjustments) of the grasping hand. However, to feed the dorsal stream with the visual properties of the target object, the brain must first select the correct object to process in relation to the intended action goal. For example, when performing your daily grasping actions, you must select the target object among an array of other objects, and you must select the appropriate action(s) to interact with it based on the intended goal. As this selection process takes place, it is essential to investigate if and how the surrounding objects interfere with the programming of the grasping action to better understand how the grasping circuit truly operates in more complex (or everyday) environments. Therefore, it is now essential to review how visual selective attention operates in relation to action planning and action selection.

Attention can be an ambiguous topic to investigate for multiple theoretical concerns (see Hommel et al., 2019), however visual selective attention can generally serve two main functions: selectively focusing on a target for the purpose to enhance its perception and selectively focusing on a target for the purpose of action planning (Allport, 1987). More specifically, visual attention can facilitate target detection (Posner, 1980), target location (Treisman, 1988), object recognition (Schneider, 1995), and visual short-term memory processing (Duncan & Humphreys, 1989) – attention as a selection-for-perception mechanism. However, visual selective attention is also utilized to extract the information needed to select and plan goal-directed actions (Allport, 1987) – attention as a selection-for-action mechanism. Using dual-task paradigms, where participants are required to execute a movement while simultaneously identifying a discrimination target, it has been shown that these two attentional functions cannot be dissociated from each other (Schneider, 1995; Deubel & Schneider, 1996). Specifically, performance on the perceptual discrimination task becomes far superior when the discrimination target is presented at the same location as the movement target compared to all other possible locations (Baldauf, Wolf, & Deubel, 2006; Baldauf & Deubel, 2008; Deubel & Schneider, 1996; Deubel, Schneider & Paprott, 1998).

Based on this line of evidence, there is a common visual attentional resource utilized for both perceptual and motor functions by selectively processing the low-level representations (striate cortex function) of the selected object (Crick & Koch, 1990; Schneider, 1995). Once the object is selected, the ventral stream will transform the information from the striate cortex to construct the conscious perception of the object while the dorsal stream will program its associated motor prototypes. Thus, selecting a target for action will enhance the perceptual processing of that target and selecting a target for perception will activate its associated action (Bekkering & Neggers, 2002; Craighero et al., 1999; Derbyshire et al., 2006; Fagioli, Hommel & Schubotz, 2007; Musseler & Hommel, 1997; Sim et al., 2015; Wenke. Gaschler, & Nattkemper, 2005; Wykowska & Schubo, 2012). This line of evidence also supports the theory of event coding (TEC) which conceptualizes how perceived events (sensory processing), and related responses (action programming) are cognitively represented into one functional representation via a common coding mechanism, known as an “event file” – the mental representation that integrates stimulus features and the accompanying responses (Hommel et al., 1998, 2001; Prinz, 1997).

Essentially, when deploying attention on a particular object there is an automatic binding of the object features and its associated responses, and once an event file has been formed it will be automatically activated whenever the corresponding stimuli (perception) or response (action) is re-encountered in the environment. Whenever an event file needs to be updated (preestablished event file does not match the task anymore. For example, an associated perception no longer equates to the same action required previously) there will be a “partial repetition cost” which will be demonstrated by producing longer RTs and more errors on a particular task; whereas if the same event file is repeated (without a need for modification) there will be a “partial repetition benefit” in which responses will be facilitated via faster RTs and less errors (Colzato et al., 2006; Mocke et al., 2020; Hommel, 1998; Hommel et al., 2001). TEC essentially assumes that perceiving a stimulus and acting upon it recruits the same representation (e.g., event file) via widely distributed networks that will integrate information processing across various brain areas, and more specifically areas in the inferior parietal cortex (Hommel, 2009; Kikumoto & Mayr, 2020; Takacs et al., 2020). TEC’s theoretical framework demonstrates why selection-for-perception and selection-for-action would be controlled by the same attentional resource even though each process relies on anatomically and functionally distinct mechanisms (Goodale and Milner, 1992, 2018).

The shared visual selective attentional mechanism for action and perception also becomes evident when investigating grasping actions. When participants are required to grasp an object while simultaneously performing a perceptual discrimination task (either at another location or the same location) they showed a delay in the opening of their hand and a delay in their grip scaling of the object's size (Hesse & Deubel, 2011; Hesse, Schenk & Deubel, 2012). This demonstrates that visual selective attention is needed for the grasping circuit to effectively optimize its computation even when only planning one action guided under full visual control. Now that we can accept the shared attentional resource between the dorsal and ventral stream functions, it is essential to investigate how visual selective attention operates when planning a goal-directed action towards a target object placed among other nontargets that could possibly interfere with the movement if captured by attention for either perceptual or motor purposes.

A study by Tipper, Lortie, and Baylis (1992) was one of the first to directly explore how selective attention operates while using a task that required participants to physically reach out and touch a target among other nontargets (as opposed to the typical forms of measurements used during that era: keypresses, verbal judgments, etc.). Their results demonstrated that participants' response time to touch an illuminated target button was greater on trials in which a distractor (non-target) was also illuminated on or near the hand trajectory relative to trials in which there was no distractor illuminated, or when distractors were illuminated far from the hand trajectory. This revealed that participants attentional resource was distributed relative to where the movement path would take place. The authors proposed that because attention is allocated to the location of where the movement will take place, this causes the nontarget within that location to be perceived which automatically elicits its associated motor plan. Since there's now multiple motor plans being processed in parallel, the response associated with the nontarget must be inhibited to successfully reach out and touch the target, hence resulting in participants having longer RTs and MTs when completing the task. Furthermore, the interference effects produced by the nontargets will change as the start location of the responding hand is varied (e.g., nontarget presented behind the target will not interfere when the hand starts in front of the target, however it will interfere if the hand starts at the back of the target) while location of the eyes, head, and shoulders remain the same (Meegan & Tipper, 1998; Tipper et al., 1992; Pratt & Abrams, 1994). This clearly shows an action-centered based attentional frame of reference since the interferences are driven by where the acting hand is situated relative to the target and nontarget.

In addition, it has been demonstrated that a specific action intention can enhance the visual processing of action-relevant features. Bekkering and Neggers (2002) instructed participants to search and saccade to a target object presented among distractors in two conditions: 1) a saccade-and-point condition, and 2) a saccade-and-grasp condition. The results revealed that orientation selection, as opposed to colour selection, was better in the saccade-and-grasp condition than the other condition. Specifically, in the grasping condition, fewer saccades were made to objects with the wrong orientation compared to the pointing condition. However, the number of saccades to an object with the wrong colour was similar in both conditions. Since object orientation (but not colour discrimination) is relevant for performing a grasping movement, the results support the view that action intentions influence visual attention at a very early stage of movement programming.

The results of these studies, which also nicely converge with Rizzolatti's et al. (1987, 1994) premotor theory of attention and the affordance theories of attention (Gibson, 1979; Michaels, 1988; Tucker & Ellis, 1998; Wallace, 1971), created a paradigm shift in how researchers conceptualized action selection. Specifically, it seems that if an object is captured by attention (even when it is not the target) it will automatically program its associated action. This view of how we process the environment is vastly different from what traditional cognitive psychology models would describe: stimulus is first identified and then the response is selected and programmed afterwards. The claim for the automatic encoding of actions gained further support when it was shown that nontargets can directly interfere with the reaching kinematics towards the target (Chapman et al., 2010; Gallivan & Chapman, 2014, Howard & Tipper, 1997; Welsh & Elliott, 2004). Specifically, reaches curve away from distractors that need to be ignored (Howard & Tipper, 1997; Tipper et al., 1998) but curve towards distractors when they can be a potential target, or when attention is cued/primed to the distractor's location (Chapman et al., 2010, Neyedli & Welsh, 2012, Tipper et al., 2002; Welsh & Elliott, 2004; Welsh, 2011). This suggests that multiple objects and their associated actions can be encoded in parallel, and this will create a competition for action execution. If the competition (or conflict) is not resolved by the time the movement is initiated, the reaching path of the movement will curve towards the distractor, whereas if the distractor-related movement plan is inhibited prior to movement initiation the reaching path will curve away from the distractor.

This aligns with the evidence from neural recordings that showed when monkeys are faced with two potential reaching targets, the directional signals representing both locations were simultaneously activated within PMd until one of the targets was cued; and once cued the corresponding neural population increased its activity while the population of neurons coding for the other location was suppressed (Cisek & Kalaska, 2005, Cisek, 2007). To further explore how this parallel processing of multiple actions take place in real-time, Chapman et al. (2010) investigated the moment-to-moment kinematics of motor decision making by having participants rapidly reach out to stimuli prior to the target being cued. It was shown that participants' initial trajectory path when faced with multiple potential targets reflected a spatial averaging that considers potential target locations and potential target probability before the movement is corrected in-flight to the cued target location. Furthermore, the spatial averaging seen when faced with target uncertainty is not driven by the visual averaging of the possible locations but by the motor averaging of the possible actions (Gallivan et al., 2017). In addition, not only can the motor plans for two potential reach targets be processed simultaneously but they can also be co-optimized: if a target that can be reached using either a wrist supination or pronation movement, participants will select the movement that is most compatible with the nontarget – and this happens outside of the participants' conscious awareness (Gallivan et al., 2015). The same effect is also shown when the potential targets are presented sequentially over time via both proactive and retroactive influence (Gallivan et al., 2016).

The evidence for the automatic encoding of action and the parallel processing of multiple actions has been clearly demonstrated when investigating reaching actions. However, what happens to the grasping hand when reaching towards a target surrounded by another nontarget? In the last section, when describing the neuroscience of the grasping circuit within the dorsal stream, it was revealed that areas responsible for controlling the grasping hand are distinct from the areas controlling its reaching kinematics. Specifically, the neural machinery of the grasping circuit specializes in accurately shaping the size and orientation of the hand's aperture to effectively grasp the target object while providing real-time adjustments (online control) as the movement takes place (Binkofski et al., 1998; Culham et al., 2003, 2006; Filmon, 2010; Fluet et al., 2010; Frey et al., 2005; Murata et al., 1997; Raos et al., 2006 Rizzolatti et al., 1988). Therefore, it is necessary to explore whether the kinematics controlling the shaping of the hand can also be vulnerable to interference by the presence of nontargets. Since it has been shown that AIP can have multiple grasping prototypes activated at the same time (Baumann et al., 2009), it makes it possible that a competition between possible grasping actions (e.g., requiring small PGA vs. big PGA) could interfere with the final action selection in a similar mechanism as seen with reaching actions (e.g., motor averaging). In addition, the grasping circuit is more interconnected with the ventral stream areas than the reaching circuit (Budisavljevic et al., 2018), so for any evidence of interference it will be necessary to investigate whether the cause is of perceptual (interference from outside the circuit) or motor nature (interference from within the circuit).

There has been human neuropsychological evidence demonstrating support for the automatic encoding of action when selecting a grasping action towards a single target. Specifically, patients with frontal lobe damage can successfully reach out for a cup with their left hand when the cup's handle is located on the left side; but when asked to reach out with their left hand for a cup with the handle located on the right side they will automatically, and incorrectly, reach out with their right hand to perform the task (Humphreys & Riddoch, 2000; Riddoch et al., 1998). This suggest the grasping circuit is automatically encoding the action of programming a righthanded grasp when the handle is located on the right-side, and because these patients have damage affecting higher-level motor areas there is no signal to trigger the inhibition of unleashing this action. This aligns with the premise that deploying attention to an object will automatically elicit its associated action, suggesting there is a possibility that the grasping system could also be vulnerable to interference from nontarget objects as seen with movement trajectories in reaching studies but in this case affecting the hand shaping kinematics.

In 1996, Castiello performed a series of studies to investigate the role of selective attention for controlling grasping actions. Castiello wanted to further explore the results found by Tipper et al. (1992) while using a more ecological approach to experimental testing. Therefore, Castillo measured participants' hand kinematics when reaching out towards a target fruit surrounded by a nontarget fruit placed at various locations. Unlike Tipper et al. (1992), it was shown that the simple presence of distractors did not impact or cause any alterations in hand kinematics when reaching for the target regardless of where the distractors were placed. However, when applying a double-task procedure, in which participants had to report how many light flicks were flashed on the nontarget fruit while maintaining fixation on the target fruit, interference effects on hand kinematics were detected. Specifically, it was shown that the size of the fruit on which the light flickered affected the size of the grip aperture used to grasp the target object. For example, if the target fruit was a cherry, participants' PGA was greater when the distracting fruit was an apple compared to when it was a mandarin. It was also found that participants' MT, time to PGA, and movement velocity was slower when the spotlight of the non-target fruit began before movement onset, suggesting that grasping actions are most vulnerable to interferences from nontarget objects during the movement planning phase.

Castiello concluded that grasping actions are less vulnerable to interference caused by nontargets relative to reaching actions. However, when attention is forced (covertly) to be allocated towards the nontarget it increases the activation (or decreases the inhibition) of its associated motor program and this leaks into the grasping plan towards the target [2]. Interestingly, the interference seems to be driven by a similar motor averaging procedure as seen with reaching studies (the combination, or averaging, of both plans) but for PGA (e.g., smaller PGA when distractor is smaller, but larger PGA when distractor is larger). This suggest that the interference is most likely driven via a competition between motor plans within the grasping circuit elicited by the attentional capture of the nontarget's intrinsic features (parallel activation of grasping type

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[2] It is important to note that we failed to replicate these findings (Coughlin, LeBlanc, & Westwood, 2016). More details will be discussed during the general discussion.

for target and for nontarget). However, these results were not only demonstrated with visual distractors but also with taste in which PGA was greater when participants reached out and grasped a small fruit (e.g., strawberry) that was preceded by a sip of a “large” (e.g., orange) relative to a “small” (e.g., almond) flavored juice (Parma et al., 2011). Grasping kinematics have also been shown to be affected by words the participants read before movement execution (e.g., words representing a larger object will cause a large PGA; Glover et al., 2004) and by the number shown on the object during grasping (e.g., larger digits will cause a larger PGA; Andres et al., 2008). This suggest that the nature of the interference can also be driven by the perceptual and/or semantic properties of the nontarget – processing happening outside the grasping circuit – which presumably triggers the associated motor plan which causes the motor interference.

Since there are only a very limited number of studies demonstrating a distractor interference effect on grasping kinematics (e.g., PGA), it is very difficult to precisely conclude how and why these interference effects emerge. However, many studies have shown that the planning of a grasping action towards an object can also be highly influenced by contextual factors (Ansuini et al., 2006, 2008; Cohen & Rosenbaum, 2004; Cole & Abbs, 1986; Gentilucci et al., 1997; Marteniuk et al., 1987; Quaney et al, 2005; Rosenbaum et al. 1990, 1992, 1993, 1996; Stelmach et al., 1994). Specifically, the way participants will pick up a dowel placed horizontally (thumb pointing to one end or the other) will depend on how the dowl is instructed to be orientated when placed in a new location (Rosenbaum & Jorgensen, 1992). Participants will essentially first produce an initial awkward grasp posture so that the final position of the hand at the end of the movement sequence will be at more comfortable state - what is commonly referred to as the end-state comfort effect (Cohen & Rosenbaum, 2004; Rosenbaum et al., 1990, 1992, 1993, 1996). The end-state comfort effect reveals that the motor system will encode the end goal (or the next step of the action) prior to programming the first segment of the action. Even with just one object, the programming of the grasping kinematics deployed to pick up the object can greatly differ based on where the object is to place afterwards.

This suggests that an integrated movement plan that incorporates all the features of the entire movement is prepared prior to initiating the first segment of the movement. This also suggests that attention is not only allocated towards the object itself but also to where and how it will be placed/used. Therefore, it seems that a more effective and ecological way to further investigate whether a current grasping action can be potentially influenced/interfered with by features of another object, that is not the immediate target, would be to utilize a task that requires sequential actions to more than one object to accomplish the end goal. After all, that is the context in which we plan and execute most of our daily actions. It is therefore essential to investigate whether the features of the second object of a sequence have any effect on the grasping kinematics towards the first object, and if so how/why. However, it is first critical to explore the literature on how sequential movements are planned and executed.

1.6 Sequential Actions

In what is now considered one of the most influential motor behaviour studies of the last century, Henry and Rogers (1960) found that the latency to initiate the first movement of an action sequence increased as the number of movements in the sequence increased even though the initial movement was the same for all sequences. Specifically, one condition simply required participants to lift their hand off a key once they heard an auditory tone. Another condition consisted of participants doing the same thing, but once they lifted their hand, they had to grasp a hanging tennis ball; and in a more complex condition participants were required to push the tennis ball away and grasp another tennis ball located to the left of the other ball. The results showed that RT of the initial action of lifting the hand off a key was performed significantly faster when completed in isolation. Moreover, RT of the initial action was also the slowest when performing the most complex sequence.

In their ‘memory drum’ account of the phenomenon, Henry and Rogers proposed that the latency in RTs associated with longer/more complex sequences reflected the fact that participants were organizing/planning more than just the first movement in the sequence prior to initiating the first movement. This study led many other researchers to further investigate what elements of the sequence contribute to this effect. It has been found that RT for the first segment of a movement sequence will increase for sequences that require longer movement durations (Klapp, 1975, 1995; Lajoie & Franks, 1997; Quinn et al., 1980; Siegel, 1986) and for sequences that require more movement segments (Chamberlin & Magill, 1989; Christina et al., 1982; Fischman, 1984; Sternberg et al., 1978). In addition, it was also shown that participants’ MT, when producing a rapid aiming movement towards a first target, took significantly longer when participants had to produce another aiming movement towards a second target, relative to when they only did the first aiming movement in isolation (Glencross, 1980). This phenomenon has been coined the one-target advantage and numerous other studies have shown similar results (Chamberlin & Magill, 1989; Christina et al., 1982; Fischman, 1984; Fischman & Liam, 1991; Fischman & Reeve, 1992; Sidaway, 1991).

These findings led to many theoretical hypotheses attempting to explain the mechanisms that causes the one-target advantage to emerge (see Bested et al., 2008 for detailed review). The online programming hypothesis proposed by Chamberlin and Magill (1989) argued that some of the programming of the subsequent movement occurs during the execution of the initial movement, thus leading to increase in movement time towards the first target. Fischman and Reeve (1992) challenged the online programming hypothesis, via various experimental manipulations, and demonstrated results in favour of their movement constraint hypothesis which explained that participants are required to constraint their movements towards the first target to ensure they meet the accuracy demands for the following movement towards the second target. However, Adam et al., (2000) performed a series of studies and developed a more refined theory called the movement integration hypothesis which combines and synthesizes ideas from both the online programming and movement constraint hypothesis – while also ruling out the possibility of other variables at play (e.g., effects of overlapping eye movements and effects of movement distance increments). Specifically, the movement integration hypothesis states that the one-target advantage phenomenon emerges as result of advance motor preparation (i.e., programming every movement segment, as an integrated movement program, prior to initiating the first response), as a result this causes the online implementation of the second movement while the first movement is executed. Since Adam et al., (2000)'s movement integration proposal, many studies have shown further supporting evidence for this explanation by applying various other experimental manipulations (Adam et al., 2001; Helsen et al., 2001; Khan et al., 2006, 2008; Van Doorn, 2008)

The one-target advantage is a robust phenomenon that persist with the occlusion of vision (Lavrysen et al., 2002) and with moderate to extensive amounts of practice (Lavrysen et al., 2003; Adam et al., 2001). It has also been demonstrated via the collection of physiological evidence. Specifically, the electromyographic (EMG) pattern of activation recoded (from six muscles acting at the shoulder) during the first pointing movement will show an increase of activation when participants are performing the movement as part of a two-tap sequence relative to a one-tap sequence (Savelber et al., 2002). The phenomenon also persists when using different limbs to execute each movement of a sequence, bolstering the idea that the one-target advantage emerges at the central level (consistent with the movement integration hypothesis) and not the peripheral level (Khan et al., 2010; Mottram et al., 2014). The only cases were the one-target advantage disappears is when performing a reversal movement as the second movement segment; since lengthening the antagonist muscle for the first reaching movement can be used to save energy when moving the limb back into the reverse direction for the second movement causing a two-target advantage instead (Adam et la., 1993; Guiard, 1993) and when the first movement requires a high demand in accuracy (Adam et al. 2000, Adam & Pass, 1996; Adam et al., 1995; Mottram et al., 2014). Based on this line of evidence, it seems that if the second movement is not a reversal movement and the first movement is not too difficult, the brain will program rapid sequential aiming movements by integrating two movement segments in which elements associated with the second movement will emerge/interfere with the execution of the first movement to enhance the transition between response elements. However, since most of the studies demonstrating the one-target advantage held the size of the second target constant, it makes it hard to decipher whether the specific features of the second target have any direct impact on the movement produce at the first target.

To address this question, Rand et al. (1997, 2000) demonstrated that changing the index of difficulty (ID) associated with the second movement (by adjusting target size and movement amplitude) can directly influence the kinematics of the first reaching movement. It was demonstrated that as the ID of the second segment increased the MT to complete the first segment increased, highlighted by a prolonged time to peak velocity and deceleration time. In addition, it was shown that the ID of the second segment had no effect on the first movement when the first movement required more accuracy (higher ID). In that case, the two segments seemed to be organized and executed in a serial manner. Thus, consistent with the movement integration hypothesis, when the first target allows for it (i.e., low accuracy demand), the planning of sequential movements is integrated into one general movement plan for the entire action sequence, and because of it the second target has a direct impact on how the first movement is programmed and executed. This explanation is also consistent with the theories surrounding the end-state comfort effect (Rosenbaum et al., 1990, 1992, 1993, 1996), and it converges nicely with the evidence demonstrating that neurons coding for a particular grasping action in AIP are heavily influenced by the subsequent motor act (Fogassi et al., 2005).

In addition, as described in section 1.5, we also know that deploying attention to an object will automatically activate its perceptual representation and associated motor prototypes. So, it seems possible that the second object can also interfere with the first movement by participants merely paying attention to the second object prior to starting the first movement and this engages the brain to process two motor plans in parallel – thus, causing interference to the first movement. In fact, it has been demonstrated that when participants are required to produce a sequential pointing movement towards an array of possible targets, they are significantly more accurate at identifying a discrimination target when presented in one of the movement target locations relative to all the other locations in between them (Baldaulf, Wolf, & Deubel, 2006). In addition, based on monkey neurophysiological evidence, the posterior parietal reach areas can encode the first and second goal for an intended double reach action in parallel (Baldauf, Cui, & Andersen, 2008). This suggest that selective visual attention can be simultaneously deployed to all the relevant action targets of a sequence, therefore making it plausible that the first action of a sequence could be interfered by the second object due to default settings of attentional capture (automatically eliciting the associated motor prototype).

Therefore, it seems that interferences found at the first movement segment of a sequence could be caused due to advanced motor preparation (programming the second action with the first action) and/or because the layout of a sequential task facilitates the deployment of attention to the second object (which implicitly activates the associated action) while programing the first action of the sequence. To further breakdown the nature of how this interference can occur, it seems it would be essential to study how the features of a second object affects the grasping kinematics towards the first object since this would allow us to directly measure what type of features (e.g., size, orientation) directly leaks into the first grasping movement (e.g., features that are only relevant to the first action vs. any type of features) and allow us to make further conclusions, that go beyond the limits of what reaching paradigms can determine, about how sequential actions are programmed.

Like reaching/pointing studies, when participants perform a sequential grasping task attention is not only allocated to the first target but also to the second target of the sequence before the onset of the initial movement, and more specifically attention is precisely deployed to the action-relevant parts of the object (Deubel & Schneider, 2004). Moreover, Ansuini et al. (2006) demonstrated that participants reaching movements to power grasp an object were faster when the object was to be lifted and placed into a large niche target area compared to a small niche target area. Also, participants shaped their hand in a more a gradual manner to match the shape of the object under the small niche condition relative to the large niche condition. Similar studies have also shown that the preshaping of the hand and placement of the fingers when grasping an object is highly dependent on the future task demands (Ansuini et al., 2008, 2009). Therefore, it seems possible that the grasping hand is also vulnerable to interferences from the features of a second object when grasping the first object within a sequential task context. It is also necessary to further explore whether these interferences will still emerge when grasping with a precision grip - as discussed in section 1.2, a precision grasp requires more online control processing than a power grip (Grol et al., 2007).

Exploring these exact questions, Hesse and Deubel (2010) instructed participants to perform a sequence consisting of grasping (with a precision grip) a cylinder, placing it into a target area, and then grasping and displacing a target bar of a certain orientation. The purpose of the experiment was to see whether the orientation of the target bar, the last movement, influenced the way in which participants grasped the cylinder. The results showed that the selected grip orientations used to grasp the cylinder were affected by the orientation in which the target bar was orientated (e.g., bar oriented to the right made participants significantly use a more rightward grip orientation when grasping the cylinder). Thus, the results suggest that each reach to grasp movements in the sequence were not performed in isolation. Moreover, it was suggested the whole action sequence was preplanned, whereby the hand orientation that would be used in the final segment was implemented during the first segment. However, by making the first placing task more difficult, the cylinder had to be placed on a small pin mounted in the center of the target area, the grip orientation towards the cylinder was not affected by the orientation of the bar. As the task was harder, the action had to be treated independently from the upcoming action. Therefore, like the studies demonstrating the one-target advantage, when the index of difficulty for the first grasping task is low, elements of the second movement will be integrated into the first grasping movement.

More specifically, in accordance with the movement integration hypothesis, Hesse and Deubel (2010) suggested that even when programming sequential grasping actions the brain engages in what they called a holistic planning process in which the first action will implement features of the second action to perform an overall more optimal and fluent action as opposed to treating each segment of the movement sequence in isolation. These results were also extended to a three-segment sequence in which the grip orientation used to place an object into various target areas was strongly adjusted to facilitate the angle the object needed to be successfully placed into the succeeding target area (Seegelke et al., 2012, 2013, 2015) – but unlike Hesse and Deubel (2010), these studies used a power grasp and the task only required the programing of one grasping action.

However, as previously explained with the reaching studies, the changes of grip orientation found by Hesse and Deubel (2010) could also be caused by deploying attention to the second object and this automatically activates its associated motor representation in parallel with the first grasping action. In particular, the automatic motor priming of the bar's associated action could have leaked into the initial movement plan. Therefore, it remains unclear whether the first action of a sequential grasping task is influenced by the properties of another object in the sequence due to holistic action planning mechanism ("strategic effect"), or because participants pay attention to the second object prior to starting the first movement and this engages the brain to process two motor plans in parallel which causes interference ("interference effect').

Based on Hesse and Deubel's (2010) results, there is no way of distinguishing between these two distinct hypotheses to gain a better understanding of the mechanisms driving the effect. However, the holistic planning hypothesis assumes that the parameters for the second action interferes with the first action in a useful way that will optimize the final action. Thus, if this view of sequential action planning is true, only the features of the second object that provide an advantage to the overall movement will interfere or be implemented within the kinematics of the first action. Therefore, we conducted a study in which we eliminated the incentive for participants to intentionally integrate the actions of a sequence (LeBlanc & Westwood, 2016). Specifically, participants were required to grasp an object and place it on its target location, followed by either grasping another object and placing it in its target area or performing a verbal size judgment about it. The size of the first object was always the same, but the second object was either bigger, smaller or the same size as the second object. We were interested to see whether PGA towards the first object would be affected by the size of the second object and whether the nature of second task (perception vs. action) played a factor. Based on the holistic planning hypothesis, PGA of the first object should not be interfered by the second object since the index and thumb must always close to the size of first object before grasping the second one. Thus, changing the magnitude of one's aperture in relation to the second object's size provides no strategic benefit (unlike grip orientation). In addition, the holistic planning hypothesis would also strongly predict against any interference seen in the perception condition since no movement is required for the second segment – there is no second movement to be integrated.

The only effect that we found was that PGA towards the first object was significantly larger when the second object was bigger, and participants performed a verbal judgment towards it. Interestingly, this was not found when performing sequential grasping actions. Although this study left us with more questions than answers (which caused the creation of this dissertation!), the only interference effect found strongly favored the attentional interference explanation since there was no second action to plan for the verbal judgment and implementing the size of the second object into the first action does not provide any movement efficiency advantage either. Therefore, in this case, it seems like deploying attention for perception towards the second object triggered its associated motor representation to be activated in parallel with the first action which interfered with the scaling of the grip aperture. This highly contradicts the assumptions behind the holistic planning and movement integration hypothesis.

However, a caveat about Hesse and Deubel's (2010) paradigm and our own paradigm (LeBlanc & Westwood, 2016) is the fact that the properties of the first object remained the same throughout the experiment. Thus, it remains possible that the participants only deployed attention to the second object since the first object remained unchanged throughout the experiment. Essentially, because the first action was always the same, the first action could have been guided by the memory of the object via ventral stream activation as opposed to being strictly guided by the real-time visuomotor control mechanisms of the dorsal stream (Westwood & Goodale, 2003; Singhal et al. 2013). This could have made the action kinematics towards the first object more vulnerable to interferences since the computations (e.g., online control) of the grasping circuit would not be optimized since the action is no longer fully guided under real-time visuomotor control. In addition, this would also facilitate the participants to deploy most of their attentional resource towards the properties of the second object while grasping the first. Therefore, to further our knowledge about the mechanisms involved in planning sequential grasping actions, it is critical to design experiments that will be enable us to distinguish between accidental (attentional interference hypothesis) and intentional action 'blending' (holistic planning hypothesis) effects while also addressing concerns about the requirements needed for the first action in the sequence.

1.7 General Research Statement

The aim of this dissertation will be to provide clarity on what specific characteristics of the second object can interfere with the kinematics of grasping the first object of a sequence; and by doing so we hope to reveal (or rule out) the possible mechanisms driving the effect. To do so, we will utilize the same paradigm as Hesse and Deubel's experiment (2010) but with two specific and very important modifications. The size of the first object (the cylinder) will be varied between two sizes on a trial-by-trial basis. This will ensure that participants are always paying attention to the first object, and this will ensure they are using real-time visuomotor control when performing the first action (optimizing the full recruitment of the dorsal stream's grasping circuit). In addition, we will also vary the size of the second object (target bar). The bar will vary between three sizes (smaller, same size, or larger than cylinder diameter) and three orientations (vertically straight, 45 ° to the right, or 45 ° to the left).

These modifications will allow us to see what type of features can influence the first action. Based on the holistic planning hypothesis, the first movement should only incorporate the orientation of the second movement since this could possibly make the overall movement more efficient or make the grasping hand better prepared for the end goal. However, the first movement should not incorporate the size of the second object since modifying the aperture between your thumb and index finger in accordance with the second object serves no strategic advantage for the overall movement goal. Whereas the attentional interference hypothesis would predict that both the orientation and size of the second object could interfere with the first action. Since the act of deploying attention towards the second object will automatically elicit its associate motor program (grip aperture and orientation), the action associated with the second object will be activated in parallel with the motor program for the first object, hence causing interference regardless of whether it is beneficial or not.

In addition, it could be that none of these hypotheses are true, and that the interference found in previous studies were due to faults in experimental designs in which the initial action was not guided under full real-time visuomotor control. The experiments within this dissertation will be controlling for this factor by varying the size of the first object. The possibility remains that perhaps the grasping circuit is less vulnerable to interference from other objects when properly activated to optimize its main functions (e.g., online corrections).

The results of my first experiment will be used as a guide on what mechanisms need to be further explored/exploited. Overall, the main goal of this dissertation will be to provide clarity on whether the first action of a sequence is indeed interfered by the features of the second object, and if so, does it happen due to matters relating to action efficiency (strategic effects) or because of an overlap in attentional capture between the first and second action (attentional interference).

1.8 References

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CHAPTER 2: INTERACTIONS BETWEEN SEQUENTIAL ACTIONS: STRATEGIC MOVEMENT PLANNING OR ATTENTIONAL INTERFERENCE?

2.1 Introduction

One of the most common actions we produce to interact with the objects in our environment is the act of grasping. As soon we initiate a reach-to-grasp movement, the aperture between our fingers already begins to reflect the size (Castiello, 2005; Jackobson & Goodale, 1991; Jeannerod 1984; Jeannerod et al., 1995) and orientation (Cuijpers et al., 2004, Glover & Dixon, 2001; Mamassian 1997) of the target object. This highlights that the programming of a grasping action heavily relies on visually processing the object's features to correctly tune the associated kinematics needed to accomplish the movement end-goal (e.g., correctly scaling one's aperture to effectively grasp and pick-up the object).

More specifically, building upon Ungerleider and Mishkin's research (1982), Goodale and Milner (1992) proposed that visual information processed via the striate cortex is projected towards two distinct streams with two different functions: the dorsal stream, covering the areas of the posterior parietal cortex, is responsible for the visual control of action (e.g., reaching out and grasping a wine glass) and the ventral stream, covering the areas of the occipitotemporal cortex, is responsible for visual perception (e.g., perceiving/recognizing the wine glass). Since its proposal, the evidence in favour of the two-visual-systems (or the perception-action model of vision) has not only grown but has continued to be refined throughout the last decade (see Goodale & Milner, 2018 for latest review).

Within the dorsal stream, connections between the AIP and PMv form the dorsolateral pathway which acts as a network (e.g., visuomotor grasping circuit) responsible for transforming the intrinsic properties of the target object into the desired motor output, such as scaling of the hand's grip aperture and orientation (Binkofski et al, 1998; Brochier & Umiltà, 2007; Castiello &

Begliomini, 2008; Culham et al., 2003; Culham & Valyear, 2006; Fagg & Arbib, 1998; Filmon, 2010; Fluet et al., 2010; Frey et al. 2005; Murata et al, 1997; Jeannerod et al., 1995; Raoes et al., 2006; Rizzolatti & Luppino, 2001; Rizzolatti & Matelli, 2003). This network specifically only codes for the absolute metrics of the target object (Ganel & Goodale, 2003). Thus, unlike perception, grasping actions are not affected by visual illusions (Agiloti et al., 1995; Ganel, Tanzer & Goodale, 2008; Haffenden & Goodale, 1998; Haffenden, Schiff, & Goodale, 2001; Hu and Goodale, 2000; Westwood, Heath, & Roy, 2000, Westwood & Goodale, 2003; Whitwell et al., 2018). In addition, the dorsolateral pathway also provides the necessary computations responsible for the real-time visual (or online) control of correcting the action (re-scaling grip aperture or adjusting grip orientation) while its being executed, and this is done outside of conscious awareness (Davare et al., 2007; Desmerget et al., 1999; Goodale et al., 1986; Pisella et al., 2000; Prablanc & Martin, 1992; Rice et al., 2006; Tunik et al., 2005).

The two-visual streams hypothesis (Goodale & Milner, 1992; 2018) has led us to gain a lot of insight about the neural mechanisms and connections required for the brain to plan, prepare and execute one grasping action to a single object. However, when we perform a goal-directed grasping action towards an object its usually embedded within a series of continuous sequential actions involving (and surrounded by) multiple objects. Therefore, it is important to investigate how the grasping circuit of the dorsal stream operates when planning two consecutive grasping actions. Specifically, does it program a distinct motor plan for each action to optimize its online control mechanisms (ensuring the most optimal kinematic approach for each action), or does it integrate both motor plans into one goal-directed action to optimize the motor approach towards the final end-goal (allowing kinematics of the first action to be strategically influenced by the second action), or do the motor plans interfere with each other (kinematics of the first action influenced by second action due to default mechanisms involving motor planning and attention).

Many studies have shown that completing an action as part of a multi-segment sequence requires more complex planning (increase in RT to complete first movement segment) and online control processing (increase in movement time to complete first movement segment) than performing the same action as a single-segment movement (Adam et al., 2000, 2001; Bested et al., 2008; Chamberlin & Magill, 1989; Christina et al., 1982; Fischman & Reeve, 1992; Henry & Rogers, 1960; Helsen et al., 2001; Khan et al., 2006, 2008, 2010, Mottram et al., 2014, Rand et al., 1997, 2000). The leading explanation to why the first movement of a sequence will be initiated and executed slower, relative to when the movement is performed in isolation, is due to preplanning the whole movement sequence in advance (i.e., programming every movement segment, as an integrated movement program, prior to initiating the first response). As a result, this causes the online implementation of the second movement while the first movement is executed to ensure the final movement is optimized. However, the great majority of evidence supporting the movement integration hypothesis used a sequential pointing task and did not explore sequential grasping actions. Since the neural substrates for controlling the hand's reaching trajectory are different than the substrates controlling the shaping of the hand (Kurata, 1993; Rizzolatti & Luppino, 2001; Davare et al., 2006), it is essential to further explore if this theory holds true when performing sequential grasping actions.

Hesse and Deubel (2010) investigated whether grasping a cylinder would be influenced by the orientation of a bar (placed vertically straight, 45 ° to the right, or 45 ° to the left) that is not the immediate target of the movement. Participants were required to grasp the cylinder, place it inside a target region, and then grasp the bar. The results showed that participants' wrist orientation when grasping the cylinder was indeed influenced by the orientation of the bar (e.g., bar oriented to the right made participants significantly use a more rightward grip orientation when grasping the cylinder). Based on this evidence, the authors suggested that the whole action sequence was planned to perform a more optimal and fluent action, as opposed to treating each segment of the movement in isolation. Evidence consistent with this idea has also been observed when participants perform an initially awkward action for earlier movement components in favor of a more comfortable posture at the end of the sequence (i.e., the end-state comfort effect; Rosenbaum et al., 1990, 1992, 1993, 1996).

However, the results found by Hesse and Deubel (2010) could also potentially be explained by an interference or 'accidental' effect as opposed to a strategic effect. Specifically, the changes of grip orientation could be due to deploying attention to the second object and automatically activating its associated motor prototype within the grasping circuit (Chao & Martin, 2000; Grèzes et al., 2003, Murata et al., 1997, Rice et al., 2007, Tucker & Ellis, 1998, 2001; Valyear et al., 2007). Thus, the automatic motor priming of the bar's associated action could have leaked into the movement plan towards the first object. Other studies have shown evidence that properties of objects that are merely distractors can influence the movement kinematics towards a target object (Bonfiglioli & Castiello, 1998; Castiello, 1996; Doyle & Walker, 2011; Howard & Tipper, 1997; Neyedli & Welsh, 2012, Tipper et al., 2002; Sheliga et al., 1994, 1995; Welsh & Elliott, 2004). It has also been found that the size of an object within a second perceptual based task (no action performed on this object) can influence PGA when grasping the first object (LeBlanc & Westwood, 2016).

There is also compelling evidence demonstrating that two different motor plans can be activated in parallel (Baumann et al., 2009; Cisek and Kalaska, 2005, 2010; Cisek 2007;

Chapman et al., 2010; Gallivan & Chapman, 2014; Klaes et al., 2011; Stewart et al., 2013, 2014, Wood et al., 2011). It has also been shown that not only can the motor plans for two potential targets be processed simultaneously, but they can also be co-optimized (Gallivan et al., 2015, 2016). Furthermore, it has been shown that when participants perform a sequential grasping task attention is not only allocated to the first target but also to the second target of the sequence before the onset of the initial movement (Deubel & Schneider, 2004). This suggest that planning sequential grasping actions could result in having two grasping plans activated in parallel when performing the first action, hence potentially causing interference to the movement kinematics. Therefore, it remains unclear whether the first action of a sequential grasping task is influenced by the properties of the second object in the sequence due to a holistic planning mechanism ("strategic effect"), or because participants pay attention to the second object prior to starting the first movement and this automatically elicits its motor prototype causing the grasping circuit to process two motor plans in parallel ("interference effect').

It is important to further define each hypothesis to highlight that the two ideas have very different purposes. The holistic planning hypothesis proposes the following: 1) an integrated movement plan with multiple distinct elements, 2) movement elements can be influenced by other movement elements in the interest of overall efficiency, 3) this is a deliberate plan that reflects the actor's overall intention/movement end-goal. In contrast, the attentional interference hypothesis proposes this alternative view: 1) series of movement elements, 2) movement elements are blended to some extent due to parallel processing, 3) this is NOT intentional, and has no deliberate intention to optimize overall efficiency although this could occur purely by accident, 4) attentional deployment towards the second object is required to produce the interference. Based on the current evidence, such as Hesse and Deubel's (2010) results, there is no way of distinguishing between these two distinct hypotheses to gain a better understanding of the mechanisms driving the effect.

In addition, a caveat about Hesse and Deubel's (2010) paradigm- and other similar studies (Haggard, 1998; LeBlanc & Westwood, 2016; Seegelke et al., 2012, 2013, 2015) - is the fact that the properties of the first object remained the same throughout the experiment. Thus, it remains possible that the participants only deployed attention to the second object since the first object remained unchanged throughout the experiment. Essentially, because the first action was always the same, the first action could have been guided by the memory of the object via ventral stream recruitment as opposed to being strictly guided by the real-time visuomotor control mechanisms of the dorsal stream (Westwood & Goodale, 2003; Singhal et al. 2013). This could have facilitated the participants to dedicate their whole attentional resource to the properties of the second object while grasping the first, hence making the meaning of their result even more unclear. To further our knowledge about the mechanisms involved in planning sequential grasping actions it is critical to design an experiment that will be able to distinguish between accidental (attentional interference hypothesis) and strategic effects (holistic planning hypothesis) while also addressing concerns about the nature of the first movement in the sequence. Therefore, we used a similar paradigm as Hesse and Deubel (2010) but with the critical addition of manipulating the size of the first and second object.

If the central nervous system does engage in holistic planning when preparing sequential grasping actions, it is hypothesized that only the orientation of the second object, not the size, will have an influence on the first action. Because the hand must always close to the size of the cylinder before grasping the second object, opening the hand wider or narrower in anticipation of the second object's size confers no obvious strategic benefit and thus any influence on the first movement would not be consistent with a key tenet of the holistic planning hypothesis which is to optimize overall movement end-goal. In contrast, the orientation of the second object can be usefully incorporated into the first grasping movement since the cylinder affords all possible hand orientations, and this could ensure a more efficient transition between the first and second action to optimize the movement-end goal (e.g., picking-up the second object). However, if the attentional interference hypothesis is correct, we predict to see effects of both size and orientation.

Furthermore, instead of having the same cylinder (first object) throughout the experiment we incorporated two possible sizes. Since the cylinder can be one of two sizes throughout the trials, this will force the participants to pay attention to the first object and to generate an appropriately scaled movement on each trial rather than providing them the opportunity to simply rely on their memory. This addition to the paradigm will ensure that the participants are deploying real-time visuomotor control towards the first object – and consequently could also possibly eliminate the previous effects found. If that is the case, it would be argued that the grasping circuit, when fully engaged, is more immune to sequential effects than previously hypothesized.

2.2 Methods

2.2.1 Participants

Nineteen undergraduate students at Dalhousie University participated in the current study in exchange for partial course credit. All were right-handed, had normal or corrected-to-normal vision, and no history of neurological deficit as ascertained by self-report. Each participant provided informed written consent prior to participation in accordance with guidelines established by the Dalhousie University Research Ethics Board.

2.2.2 Materials

For each trial of the experiment, two objects were presented simultaneously on a white surface table. The stimulus for the first action of the task was a black cylinder located 20cm to the left of the starting switch. The height of the cylinder (5cm) remained the same throughout the experiment, however the diameter varied between 5cm and 6 cm on a trial-to-trial basis. Twenty centimeters above the location of the cylinder was a marked black circle (7cm diameter). This indicated the target location of where the participants needed to move the cylinder. The stimulus for the second action of the task was a black rectangle bar located 20 cm to the right of the target circle. The width and height of the bar remained the same throughout the experiment (2cm x 2cm). However, the size and orientation changed on a trial-to-trial basis. For each cylinder size the second object could either be smaller (3cm, 4cm), the same size (5cm, 6cm) or bigger (7cm, 8cm) and could be orientated vertically straight, 45 ° to the right, or 45 ° to the left – see Figure 1 for an example of the stimulus layout.

An Optotrak 3020 (Northern Digital, Waterloo, ON, CANADA) system was used to record at 200 Hz the three-dimensional locations of IREDs placed on the distal phalanx of the thumb, the lateral surface of the distal phalanx of the index finger, and the styloid process of the radius of the right upper limb. Participants wore liquid–crystal occlusion glasses (PLATO Translucent Technologies, Toronto, ON, Canada) to block visual input during the experiment as indicated in the procedure. A tone was presented as the signal for participants to initiate the first action (800 Hz; 250 ms).

2.2.3 Procedure

Participants were seated in front of a table during all experimental trials. Each participant performed several practice trials to ensure they understood the requirements of the task. They were first instructed to depress a release button using their pinched right index finger and thumb

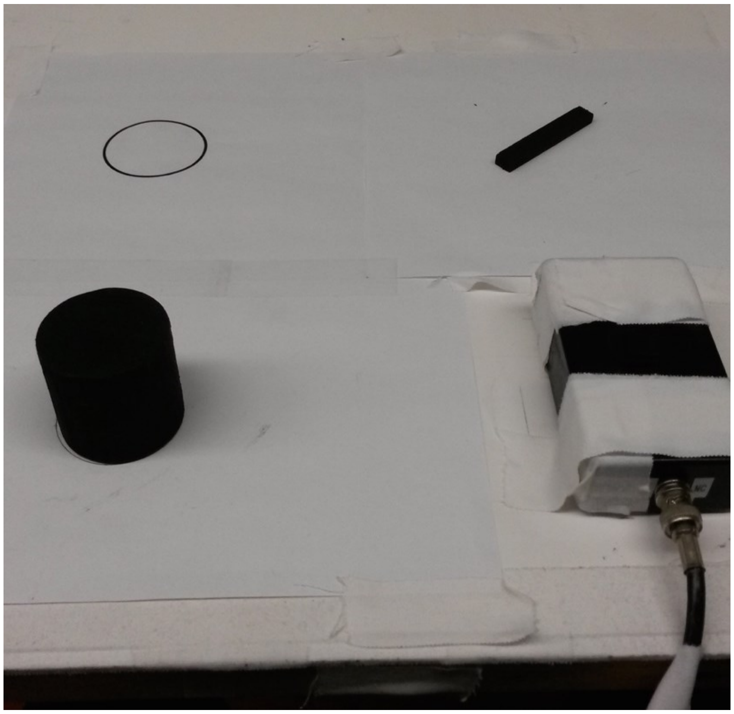

Figure 1. Stimulus layout. This example depicts a trial where the second object is longer than the cylinder's diameter and is titled towards the right.

at the start of each trial. The LCD glasses were opaque at the start of each trial while the experimenter positioned the target objects. Once the objects were correctly positioned the experimenter triggered the start of the trial and the glasses turned transparent to reveal the environment. The start tone was presented 500-1500 ms after (possible delays were 500, 750, 100, 1250, or 1500 ms with equal distribution and randomized trial by trial).

At the sound of the start tone, participants were required to reach, grasp, and pick up (with right thumb and right index finger) the cylinder and to place it in the marked target circle area. Once the first action was completed participants were then required to reach, grasp, and pick up the rectangular bar along the front-to-back axis and place it in the center of the workspace. Participants were instructed to complete each action as quickly and accurately as possible. The LCD glasses returned to an opaque state 5000ms after the initiation tone, such that vision was available during the entire task but occluded at the end of each trial before the stimuli for the next trials were arranged. Each participant performed a total of 180 trials (90 trials for each type of cylinder and ten trials for each possible size and orientation combinations).

2.2.4 Data Processing

Offline, a custom Python routine was used to extract movement kinematics from the raw 3D data collected during the experiment. The data was filtered using a second-order dual pass Butterworth filter employing a low-pass cut-off frequency of 12Hz. Measures extracted from the primary action (the movement to the first object) included peak grip aperture (PGA; the maximum distance between the index finger and thumb achieved during the movement), reaction time (RT; the time from the onset of the auditory go signal until the velocity of the IRED on the wrist exceeded 30 mm/s for 5 consecutive time samples), movement time (MT; the time from when the wrist IRED exceeded 30 mm/s for 5 consecutive time samples until it dropped below 30 mm/s for 5 consecutive time samples), and grip orientation (the angle of the horizontal projection of the index finger and thumb – 0 ° in orientation corresponded to a perfect sagittal line projection, clockwise projections from that line is defined as positive angles and anticlockwise projections as negative angles). Interactive routines enabled the experimenter to ensure the automated algorithms chose the appropriate values in cases of missing IRED positions. All dependent measures were analyzed within participants, and trials were rejected if any of the measures fell beyond ±3 standard deviations of the individual participants' mean for that measure (less than 1% of trials were rejected from data analyses).

Each dependent measure was analyzed using a 2 (cylinder size) x 3 (rectangular bar size) x 3 (rectangular bar orientation) ANOVA ($\alpha = 0.05$). Post hoc analysis was done with

Bonferroni-corrected t tests. Sphericity was evaluated using Mauchly's test ($\alpha = 0.05$), and Greenhouse–Geisser corrections were applied if needed.

2.3 Results

2.3.1 Peak Grip Aperture

The results revealed no significant interaction between the size of the cylinder's diameter (first object), size of rectangular object (second object) and orientation of rectangular object (second object), $F\ (4,72) = 1.49$, $p = 0.22$, $\eta_p^2 = 0.09$. There was also no significant interaction between the size of first object and size of second object, $F\ (2, 36) = 0.25$, $p = 0.78$, $\eta_p^2 = 0.02$; the size of first object and orientation of second object, $F\ (2, 36) = 0.68$, $p = 0.52$, $\eta_p^2 = 0.04$; the size of second object and orientation of second object, $F\ (4, 72) = 0.28$, $p = 0.89$, $\eta_p^2 = 0.02$. As expected, there was a main effect for size of first object, $F\ (1,18) = 406.01$, $p < 0.001$, $\eta_p^2 = 0.96$. Participants reached out with a larger peak grip aperture for the cylinder that had a diameter of 6cm (M= 87.07mm, SE=0.11) than the one of 5cm (M=81.04mm, SE = 0.12). A main effect was also found for the size of the second object, $F\ (2, 36) = 6.02$, $p=0.006$, $\eta_p^2 = 0.29$. Post-hoc analysis (Bonferroni correction) revealed a significant difference between the smaller second object in comparison to the same size ($p=0.03$) and the larger size ($p=0.02$) but no difference between the same size and the larger size ($p = 1$). As seen in Figure 2, participants reached out for the first object with a smaller peak grip aperture when the second object was smaller than the first one (M =83.76mm, SE= 0.14) relative to if the second object was the same size (M=84.32mm, SE=0.13) or larger (M=84.24mm, SE=0.14). No main effect of orientation of second object was found, $F\ (2,36) = 0.49$, $p=0.61$, $\eta_p^2 = 0.03$.

2.3.2 Grip Orientation

No significant interaction was found between size of first object, size of second object and orientation of second object, $F\ (4,72) = 1.15$, $p=0.34$, $\eta_p^2 = 0.07$. There was also no significant interaction between size of first object and size of second object, $F\ (2, 36) = 0.85$, p

$=0.44$, $\eta_p^2 = 0.05$, size of first object and orientation of second object, F (2,36) = 0.004, p= 0.99, $\eta_p^2 = 0.001$ and size of second object and orientation of second object, F (4,72) = 0.88, p=0.48, $\eta_p^2 = 0.05$. A main effect of size of the first object was revealed, F (1,18) = 14.6, p =0.002, $\eta_p^2 =$ 0.49, participants tilted their grip orientation more towards the left for the small cylinder (M= -4.09 °, SE = 0.22) than the large cylinder (M = -2.79 °, SE=0.21). No main effect of size of second object, F (2,30) = 0.6, p= 0.55, $\eta_p^2 = 0.04$ and most importantly no main effect of orientation of second object, F (2,36) = 0.56, p= 0.58, $\eta_p^2 = 0.03$, as seen on Figure 3.

2.3.3 Reaction Time

No significant interaction was found for size of the first object, size of the second object and orientation of second object, F (4,72) = 0.63, p = 0.64, $\eta_p^2 = 0.04$. No significant interaction between size of first object and size second object, F (2,36) = 1.79, p = 0.18, $\eta_p^2 = 0.11$, size of first object and orientation of second object, F (2,36) = 0.31, p = 0.73, $\eta_p^2 = 0.02$, and size of second object and orientation of second object, F (4,72) = 0.45, p = 0.77, $\eta_p^2 = 0.03$. No main effect of size of the first object, F (1,18) = 0.001, p =0.98, $\eta_p^2 = 0.001$, size of second object, F (2,36) = 0.02, p =0.98, $\eta_p^2 = 0.001$ and orientation of second object, F (2, 36) = 0.5, p =0.61, η_p^2 = 0.03.

2.3.4 Movement Time

No significant interaction was found for size of the first object, size of the second object and orientation of second object, F (4,72) = 1.72, p =0.16, $\eta_p^2 = 0.10$. No significant interaction between size of first object and size of second object, F (2,36) = 2.76, p =0.09, $\eta_p^2 = 0.15$, size of first object and orientation of second object, F (2,36) = 3.2, p =0.08, $\eta_p^2 = 0.16$, size of second object and orientation of second object, F (4,72) = 1.3, p= 0.28, $\eta_p^2 = 0.08$. No main effect of size of first object, F (1,18) = 0.02, p =0.89, $\eta_p^2 = 0.001$, size of second object F (2, 36) = 0.4, p = 0.67, $\eta_p^2 = 0.03$ and orientation of second object, F (2,36) = 0.35, p=0.71, $\eta_p^2 = 0.02$.

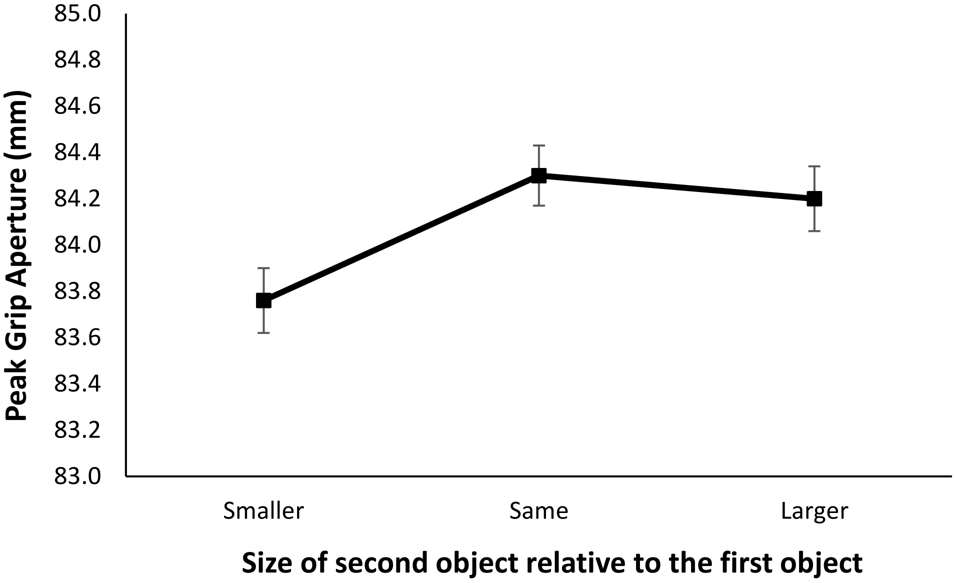

Figure 2. Mean peak grip aperture when performing a grasping action to the first object in relation to the size of the second object. Error bars indicate SEM. As shown, PGA for the first action is significantly smaller when the second object is smaller relative to when the second object is the same size or larger than the first object.

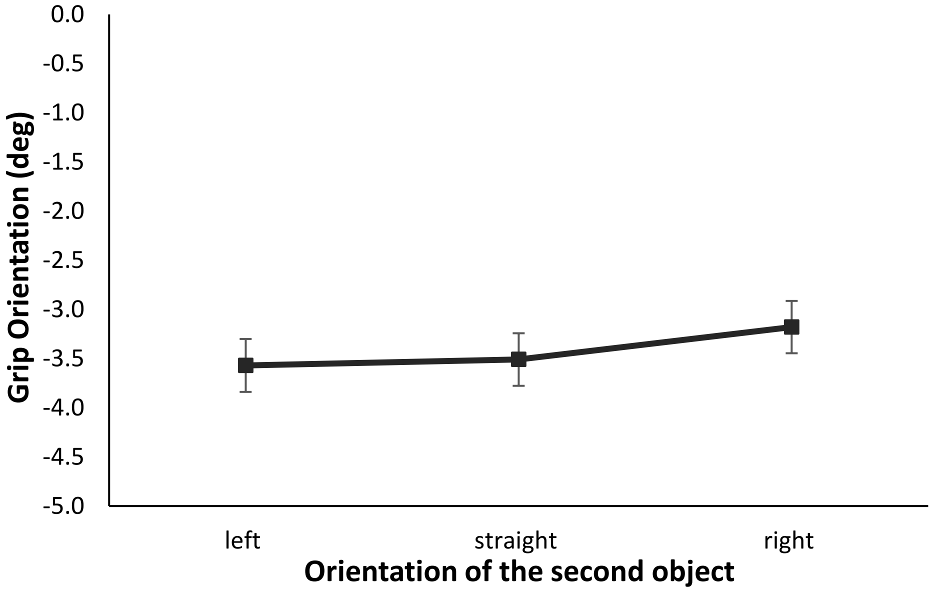

Figure 3. Mean grip orientation when performing a grasping action to the first object in relation to the orientation of the second object. Error bars indicate SEM. No significant differences were found.

2.3.5 Time to Peak Grip Aperture

No significant interaction was found for the size of the first object, size of the second object and orientation of second object, $F(4, 72) = 1.2$, $p = 0.31$, $\eta_p^2 = 0.07$. No significant interaction between size of first object and size of second object, $F(2,36) = 1.82$, $p = 0.18$, $\eta_p^2 = 0.11$, no interaction for size of second object and orientation of second object, $F(2, 36) = 0.41$, $p = 0.80$, $\eta_p^2 = 0.03$, and no interaction was found for size of first object and orientation of second object, $F(2, 36) = 1.65$, $p = 0.21$, $\eta_p^2 = 0.09$. No main effect of size of first object, $F(1,18) = 0.39$, $p = 0.54$, $\eta_p^2 = 0.54$, size of second object, $F(2, 36) = 0.29$, $p = 0.75$, $\eta_p^2 = 0.02$ and orientation of second object, $F(2, 36) = 0.40$, $p = 0.67$, $\eta_p^2 = 0.03$.

2.4 Discussion

The purpose of this study was to gain a better understanding about how we program and execute sequential grasping actions. We were particularly interested to see how the kinematics of the first grasping action towards the first object is influenced by the properties of the second object within a sequence. Our results demonstrated that when participants reached out and grasped a cylinder their PGA was affected by the size of the second object in the sequence but not its orientation. More specifically, we showed that when the size of the second object was smaller than the diameter of the cylinder participants reached out with a smaller PGA compared to when the second object was either the same size or larger than the diameter of the cylinder. However, contrary to previous findings (Hesse & Deubel, 2010), our results showed that the orientation of the second object did not influence participants' grip orientation when grasping the cylinder.

Although our study was designed based on Hesse and Deubel's paradigm, we incorporated two potential sizes for the first object, the cylinder, that was randomized on a trial-by-trial basis and for each cylinder we added three corresponding sizes for the second object (smaller than the cylinder's diameter, same size, or larger) that was also randomized on a trial-by-trial basis in addition to its orientation (vertically straight, tilted to the left, or tilted to the right). One of our main concerns about Hesse and Deubel's results (2010) was the fact that the same cylinder was used throughout the experiment. It is for this reason we incorporated two different sizes of cylinder to ensure that participants were actively processing and engaging in real-time visuomotor control (e.g., fully optimizing the grasping circuit) towards the first object on each trial. The reason for incorporating the different sizes for the second object was to decipher whether the programming of the first action is only influenced by features (e.g., orientation) of the second object that can benefit the transition towards the final movement end-goal (strategic interference effects), or whether the first action can also be influenced by features (e.g., size) that serve no strategic benefit to the overall movement sequence (attentional interference effects).

We specifically predicted that if our results supported the holistic planning hypothesis only the orientation of the second object should be incorporated into the first movement and not the size. Since the cylinder affords all possible grip orientations to correctly grasp it, the orientation of the second object can be usefully incorporated into the first action to optimize the overall efficiency of the sequence of actions. Whereas, incorporating the second object's size provides no obvious strategic benefit towards the efficiency of the action. After all, the hand must always close to the cylinder's size before grasping the second object, hence blending the size of the second object into the first action by opening the hand wider or narrower provides no biomechanical advantage towards optimizing the sequence of actions. The fact that our results showed that the kinematics of the first action was affected by the size but not the orientation of the second object does not support the holistic planning hypothesis.

One possible explanation to why we failed to find an orientation effect could be because we did not use the same first object throughout the study. Previous studies that have shown orientation effects (Haggard, 1998; Hesse & Deubel, 2010; Seegelke et al., 2012, 2013, 2015) on the first action of a sequence used the same object throughout the study. This further validates our argument that when the first object of a sequence is left unchanged participants are more likely to deploy their attention towards the second object since they know what to expect for the first action, thus allowing the first action to be controlled via memory-guided mechanisms as opposed to real-time visuomotor mechanisms (Westwood & Goodale, 2003; Singhal et al. 2013). This line of reasoning is also supported by the second experiment in Hesse and Deubel's study (2010); when the first action requires more precision the orientation of the second object does not influence the action. Rand and Stelmach (2000) also found that when the initial movement segment has a high index of difficulty, the following segments are processed separately and treated as discrete actions. Although the difficulty of the first action remained the same throughout our study, participants still had no choice to actively process the first object since its size varied on trial-by-trial basis. One could potentially argue that this was enough to discourage participants' attention to be deployed towards the second object, hence explaining why no orientation effect was found. However, the fact that we did find a size effect suggest otherwise.

Unlike the holistic planning hypothesis, we predicted that if both the size and the orientation of the second object influenced the first action our results would support the attentional interference hypothesis. This hypothesis stems from the fact that it has been shown that properties of objects that are merely distractors can influence the movement kinematics towards a target object (Bonfiglioli & Castiello, 1998; Castiello, 1996; Doyle & Walker, 2001; Howard & Tipper, 1997; Neyedli & Welsh, 2012, Tipper et la., 2000; Sheliga et al., 1994, 1995;

Welsh & Elliott, 2004) and the fact that motor plans for different targets can be processed in parallel (Cisek and Kalaska 2005, 2010; Chapman et al. 2010, Gallivan & Chapman, 2014, Gallivan et al., 2015, 2016; Klaes et al. 2011; Stewart et al., 2013, 2014, Tipper et al., 1998, Wood et al., 2011). Therefore, if the participants deployed attention towards the second object before executing the first action each action would be processed simultaneously, and the features (both orientation and size) of the second object would potentially influence the motor programming (PGA and grip orientation) of the first grasping action. Partial support for the attentional interference hypothesis was found since participants kinematics of the first action was influenced by the size of the second object – albeit only when the second object was smaller.

One possible reason we found a size effect but not an orientation effect could be because the size of the first object also varied (and had no orientation feature) – interference due to shared features between action plans (Hommel, 2004, Fournier et al., 2014, Mattson & Fournier, 2008; Stoet & Hommel, 1999). Since the participants had to pay attention to the size feature of the first object it could have automatically made the size of the second object more salient relative to its orientation, hence causing more interference with the size scaling of the first grasping action. However, it remains unclear why we only found this effect for the smaller object and not the larger one. One possibility could be that preparing a future action towards a smaller object will require more online control than the initial action towards a larger object (see Grol et al. 2007). Consequently, more attentional resource is dedicated towards the second action, and this causes its associated size prototype to interfere with the size scaling of the first grasping action – something that does not happen when the second object is larger or the same size.

One way to further explore the nature of this specific interference would be to explore whether we would get a similar interference effect if participants were to perform a perceptual task for the second object (no action required). Essentially, if the unique interference we found is solely driven by the fact that the smaller second object requires more online control, this interference effect should be eliminated if no action is required – even though the second object will still be present and part of the overall sequence but as a perceptual based task (still needs to be actively processed). Furthermore, this design would also allow to us to further investigate whether the interference effect is purely driven by motor processing or whether it can potentially be driven by perceptual mechanisms via cross communication between the ventral and dorsal pathways (Budisavljevic et al., 2018, Cloutman, 2013; De Haan & Cowey, 2011; Goodale, 2014; Milner, 2017; Gallivan et al., 2016, Schenk & McIntosh, 2010; van Polanen & Davare, 2015). It remains possible that by simply perceiving the second object it could interfere with the programming of the action towards the first object in a similar manner, as we demonstrated in one of our previous studies (LeBlanc & Westwood, 2016). If that is the case, it would further disprove the holistic planning hypothesis since there is only ever one sole action to plan (no multiple actions to effectively integrate). In contrast, this would give further support to the attentional interference hypothesis in which simply paying attention to the second object, whether it is for perceptual or motor purposes, will automatically (unconscious processing) elicit its associated motor prototype (Chao & Martin, 2000; Grèzes et al., 2003; Murata et al., 1997; Rice et al., 2007; Rizzolatti & Luppino, 2001; Tucker & Ellis, 1998, 2001; Valyear et al., 2007) causing interference to the first grasping action.

In conclusion, we showed that the size of the second object within a sequence influenced the magnitude of the participants grip aperture towards the first object only when the second object is smaller, whereas the orientation of the second object had no effect on how participants scaled their grip orientation onto the first object. Based on these results, we can conclude that when the features of both the first and second object change on a trial-by-trial basis participants do not engage in the holistic planning approach as suggested by previous literature (Haggard, 1998; Hesse & Deubel, 2010; Seegelke et al., 2012, 2013). Furthermore, because incorporating the size of the second object into the first action serves no biomechanical advantage to the overall completion of the action sequence (unlike the orientation feature), our results demonstrate that when planning sequential actions, features of the second object can still interfere with the first movement regardless of whether it serves an advantage to the whole movement or not.

2.5 References

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CHAPTER 3: EFFECTS OF AN UPCOMING PERCEPTUAL BASED TASK ON GRASPING

3.1 Introduction

Many of our daily tasks are successfully accomplished by the act of performing a sequence of coordinated grasping actions. Although we know a lot about the neuroscience of how the brain plans one grasping action towards one single object (as highlighted by reviews from Castiello, 2005, Castiello & Begliomoni, 2008, Grafton, 2010, Turella & Lingnua, 2014), there are many unsolved mysteries surrounding how the central nervous system programs two consecutive grasping actions involving two different objects. More specifically, how can features (e.g., size, orientation) of the second object of a sequence (the future action) directly influence the grasping kinematics towards the first object (the immediate action)?

Hesse and Deubel (2010) showed that participants' grip orientation used to grasp the first object of sequence (a cylinder) was highly influenced by the orientation of the object associated with the final action (e.g., second object oriented to the left made participants significantly use a more leftward grip orientation when grasping the first object). Their results were framed in the context that the brain engages in holistic planning when programing sequential grasping actions. Thus, as opposed to treating each action of the sequence in isolation, the whole sequence is programmed together and features of the second action will be implemented within the first action to optimize the movement end-goal (e.g., grip orientation already pre-adjusted to perform the final action as the first action takes place). This explanation also nicely converges with the movement integration hypothesis used to explain the one-target advantage when performing sequential reaching actions (Adam et al., 2000, 2001; Bested et al., 2018; Helsen et al., 2001; Khan et al., 2006, 2008, 2010, Mottram et al., 2014, Rand et al., 1997, 2000) and the end-state comfort effects seen in grasping movements (Rosenbaum et al., 1990, 1992, 1993, 1996).

However, the results by Hesse and Deubel (2010) could also be explained via an attentional interference effect. It has been shown that properties of objects that are merely distractors can influence the movement kinematics towards a target object (Bonfiglioli & Castiello, 1998; Castiello, 1996; Doyle & Walker, 2011; Howard & Tipper, 1997; Neyedli & Welsh, 2012, Tipper et la., 2002; Sheliga et al., 1994, 1995; Welsh & Elliott, 2004), attention can be simultaneously deployed to all relevant action targets of a sequence (Baldaulf, Wolf, & Deubel, 2006; Baldauf, Cui, & Andersen, 2008), paying attention to an object will automatically activate its associated action (Chao & Martin, 2000; Grèzes et al., 2003, Murata et al., 1997, Rice et al., 2007, Tucker & Ellis, 1998; Valyear et al., 2007), and motor plans for different targets can be processed in parallel (Cisek and Kalaska 2005, 2010; Chapman et al. 2010, Gallivan et al., 2015, 2016; Klaes et al. 2011; Stewart et al., 2013, 2014, Tipper et al., 1998, Wood et al., 2011). Therefore, the results by Hesse and Deubel (2010) could be driven by the fact that participants deployed attention towards the second object prior to initiating the first movement, and this automatically activated its associated motor prototype (e.g., specific grip orientation) causing interference with the programming of the first action.

To clarify Hesse and Deubel's (2010) results and to give us a better understanding about how sequential grasping actions are programmed, we conducted a study (see chapter 2) using the same paradigm but added three possible sizes (in addition to the three possible orientations) for the second object. We argued that if the holistic planning hypothesis is true the first action should only be influenced by the orientation of the second object and not its size. After all, grasping a cylinder can afford to be grasped by any type of grip orientation, so incorporating the orientation of the second action into the first action could better serve the final action without impairing the first action. However, incorporating the size of the second object into the first movement serves no strategic advantage to the overall end-goal. In contrast, if the attentional interference hypothesis is true, both size and orientation should interfere with the first action since the interference is driven via an accidental effect not a strategic effect. In addition to adding sizes to the second object, we also randomized the size of the first cylinder on a trial-by-trial basis (two potential sizes) to ensure we were measuring kinematics of an action fully guided by real-time visuomotor mechanisms (Davare et al., 2007; Desmerget et al., 1999; Goodale et al., 1986; Pisella et al., 2000; Prablanc & Martin, 1992; Rice et al., 2006; Tunik et al., 2005; Westwood and Goodale, 2003). Specifically, in Hesse and Deubel's study (2010) and other studies that showed sequential effects (Haggard, 1998; Seegelke et al., 2012, 2013) the first object was always the same. This could have facilitated the participants to deploy most of their attentional resource towards the second object since they knew what to expect for the first object, hence making the meaning of the results even less clear.

Our results (see section 2.2) showed that the only feature that affected how the participants reached out to grasp the first object was the size of the second object. Specifically, when the second object's length was smaller than the diameter of the cylinder, participants reached out with a smaller PGA when grasping the cylinder relative to when the second object's length was the same size or larger than the cylinder's diameter. However, unlike Hesse and Deubel (2010), the orientation of the second object did not influence the grip orientation used to grasp the first object. Since we ensured that participants needed to pay attention to the first object by randomizing its size, participants were now fully engaging the grasping circuit's online control mechanisms to its full potential – unlike grasping the same object throughout the full experiment which could facilitate a reliance on the memory mechanisms of the ventral stream

(Westwood & Goodale, 2003; Singhal et al. 2013). As a result, the first action was no longer influenced by the orientation feature of the second object.

Nevertheless, the first action was still influenced by the size of the second object. It could be argued that since we varied the size of the first object, but not it's orientation, the size of the second object becomes more salient and this causes interference due to shared features between action plans (Hommel, 2004, Fournier et al., 2014, Mattson & Fournier, 2008; Stoet & Hommel, 1999). However, this explanation cannot explain why we only see a size effect for the smaller second object and no effect when the second object is larger. Another possible explanation for this unique effect could be driven by the fact that grasping a smaller object will require more online control (e.g., increased effective connectivity within the dorsolateral grasping circuit) relative to grasping a larger object (Grol et al., 2007). Thus, when the second object is smaller participants might require greater motor planning towards the second action relative to the first action and this causes interference when deploying the first grasping action by making PGA smaller.

One simple way that would easily disprove this explanation would be to see if we get the same effect when using the same paradigm but instead of performing a second grasping action participants would perform a perceptual judgment task for the second object. Essentially, if our previous finding was solely driven by the fact that more online control is required for the second action, the size effect should disappear if no action is required for the second object. However, if the effect is driven by attention (as opposed to motor planning) we should get the same effect since even though no action is required for the second object, participants will still need to actively process it to successfully complete the perceptual task and as a result this will automatically activate the associated motor representation (e.g., grip aperture) and interfere with the first action.

Using a perceptual based task for the second sequence instead of an action will serve as good way to investigate what (if any) interference effects emerge even when no action is required for the second sequence of this specific paradigm. This will allow us to gain further knowledge about the possible mechanisms that were at play in previous reported sequential action effects (Haggard, 1998; LeBlanc & Westwood, 2016; Seegelke et al., 2012, 2013). Specifically, the holistic planning hypothesis would predict no interference effects in this case since there is only one action to plan within this sequence (no multiple movements to integrate). We also realize that to perform the perceptual task participants will rely on neural networks of the ventral visual stream (Goodale & Milner, 1992, 2018). Although the ventral (vision-for-perception) and dorsal (vision-for-action) visual streams have distinct neuroanatomical and functional properties (Westwood and Goodale, 2011), the grasping circuit of the dorsal stream has multiple connections with areas located in the ventral stream (Budisavljevic et al., 2018). Therefore, it will also be important to investigate for any interference effects driven strictly by perceptual processing. It is possible that the perception of the object itself (independent of its action representation) could cause interference towards the first action by means of a size-contrast illusion. For example, if the second object is smaller it could make the cylinder appear larger since ventral stream processing relies on allocentric coding mechanisms (Ganel & Goodale, 2003; Goodale & Humphrey, 1998), hence participants would reach with a larger PGA – not smaller - when performing the first action.

3.2 Methods

3.2.1 Participants

Fifteen undergraduate students at Dalhousie University participated in the current study in exchange for partial course credit. All were right-handed, had normal or corrected-to-normal vision, and no history of neurological deficit as ascertained by self-report. Each participant provided informed written consent prior to participation in accordance with guidelines established by the Dalhousie University Research Ethics Board.

3.2.2 Materials

Same materials and set-up as our previous experiment (see section 2.2.2)

3.2.3 Procedure

The procedure for the first action was the same as our previous experiment (see section 2.2.3), however once the participants completed the first action, they did not perform an action towards the second object. Instead, they were required to verbalize to the experimenter the orientation and size of the second object. For example, if the second object was titled towards the right and longer than the first object, the participants would state: “Right and Longer”. Once they verbalized their perceptual judgment, they were required to return to the start switch and wait for the start of the next trial. This type of perceptual judgment, although not challenging, ensured that the participants were indeed deploying attention towards the second object (even though no second action was performed). If participants provided an incorrect judgement, that trial was excluded from the analysis. Out of 15 participants x 180 trials, this only happened a total of four times (each time was due to a size misjudgment).

3.2.4 Data Processing

Data processing followed the same procedures as our first experiment (see section 2.2.4).

3.3 Results

3.3.1 Peak Grip Aperture

The results showed no significant interaction between the size of the cylinder’s diameter (first object), size of rectangular object (second object), and orientation of the rectangular object (second object), F (4, 56) = 0.68, $p = 0.61$, $\eta_p^2 = 0.06$. There was also no significant interaction between the size of the first object and size of the second object, F (2, 28) = 0.14, $p = 0.87$, $\eta_p^2 = 0.01$; the size of the first object and orientation of second object, F (2, 28) = 0.66, $p = 0.53$, $\eta_p^2 = 0.06$; the size of the second object and the orientation of the second object, F (4, 56) = 1.2, $p = 0.32$, $\eta_p^2 = 0.09$. As expected, there was a main effect for size of the first object, F (1, 14) = 71.63, $p < 0.001$, $\eta_p^2 = 0.88$. Participants reached out with a larger PGA for the larger cylinder (M = 83.86 mm, SE = 0.14) than the smaller cylinder (M = 79.01, SE = 0.13). A main effect of size for the second object was also found, F (2, 28) = 3.43, $p = 0.05$, $\eta_p^2 = 0.24$. Post-hoc analysis (Bonferroni correction) revealed a significant difference between the smaller second object in comparison to the same size ($p=0.004$) and the larger size ($p=0.01$) but no difference between the same size and the larger size ($p = 1$). As seen in Figure 4, participants reached out for the first object with a smaller peak grip aperture when the second object was smaller than the first one (M= 80.95mm, SE= 0.17) relative to if the second object was the same size (M=81.7mm, SE=0.16) or larger (M=81.66mm, SE=0.17). No main effect of orientation of second object was found, F (2,28) = 0.96, $p=0.4$, $\eta_p^2= 0.08$.

3.3.2 Grip Orientation

No significant interaction was found between size of first object, size of second object and orientation of second object, F (4,56) = 1.09, $p= 0.38$, $\eta_p^2 = 0.09$. There was also no significant interaction between size of first object and size of second object, F (2, 28) = 0.13, $p =0.88$, $\eta_p^2= 0.01$, size of first object and orientation of second object, F (2, 28) = 0.48, $p= 0.62$, $\eta_p^2= 0.04$ and size of second object and orientation of second object, F (4, 56) = 0.93, $p=0.45$, $\eta_p^2= 0.08$. No main effect of size of the first object, F (1, 14) = 0.5, $p = 0.49$, $\eta_p^2 = 0.04$; size of the second object, F (2, 28) = 0.4, $p = 0.67$, $\eta_p^2 = 0.04$; and no main effect of orientation of the second object, F (2,28) = 0.95, $p = 0.4$, $\eta_p^2 = 0.08$ as seen in figure 5.

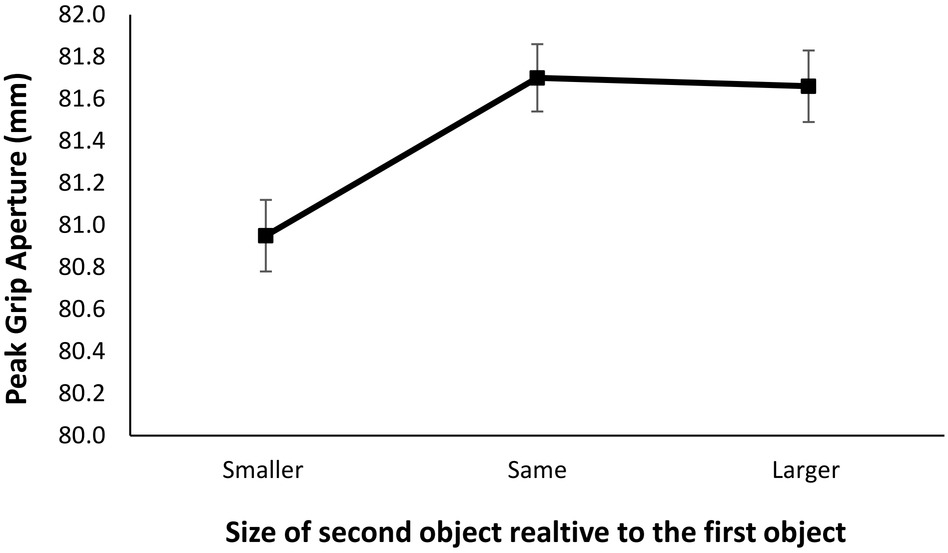

Figure 4. Mean peak grip aperture when performing a grasping action to the first object in relation to the size of the second object. Error bars indicate SEM. As shown, PGA for the first action is significantly smaller when the second object is smaller relative to when the second object is the same size or larger than the first object.

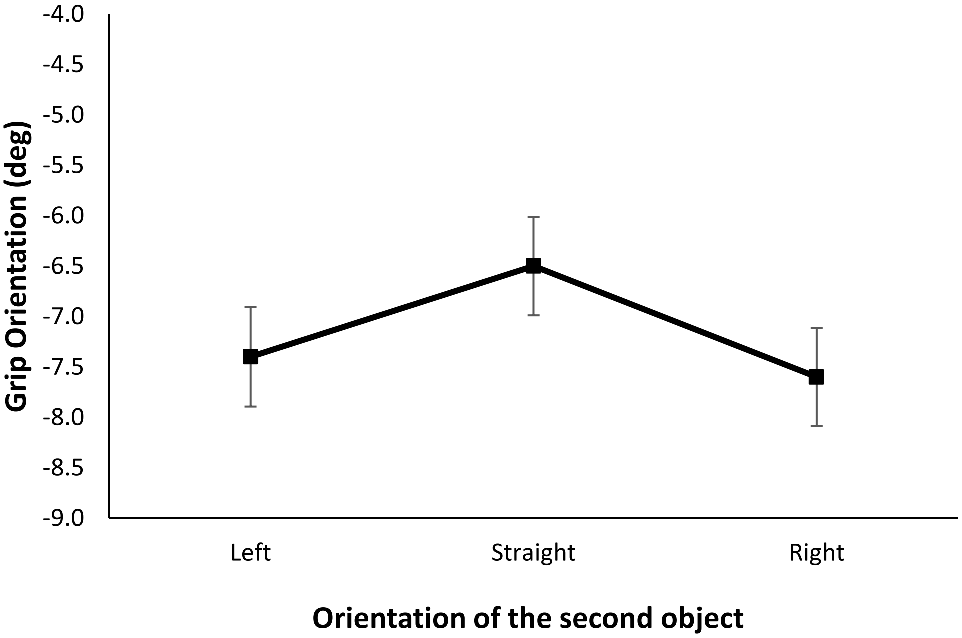

Figure 5. Mean grip orientation when performing a grasping action to the first object in relation to the orientation of the second object. Error bars indicate SEM. No significant differences were found.

3.3.3 Reaction Time

No significant interaction was found for size of the first object, size of the second object and orientation of second object, F (4, 56) = 1.8, p = 0.14, η_p^2 = 0.14. No significant interaction between size of first object and size second object, F (2, 28) = 0.51, p = 0.61, η_p^2= 0.04, size of first object and orientation of second object, F (2, 28) = 1.62, p = 0.22, η_p^2= 0.13, and size of second object and orientation of second object, F (4,56) = 0.24, p = 0.92, η_p^2 = 0.02. No main effect of size of the first object, F (1,14) = 0.07, p =0.79, η_p^2= 0.01, size of second object, F (2, 28) = 1.15, p =0.34, η_p^2 = 0.09, and orientation of second object, F (2, 28) = 1.1, p =0.35, η_p^2 = 0.09.

3.3.4 Movement Time

No significant interaction was found for the size of the first object, size of the second object and orientation of the second object, F (4, 56) = 0.81, p = 0.53, η_p^2 = 0.07. No significant interaction between size of first object and size of second object, F (2, 28) = 1.98, p = 0.16, η_p^2 = 0.15, and size of second object and orientation of second object, F (2, 28) = 1.46, p = 0.23, η_p^2 = 0.12. However, a significant interaction was found between the size of the first object and the orientation of the second object, F (2, 28) = 3.99, p = 0.03, η_p^2 = 0.27. Post-hoc analysis (Bonferroni correction) revealed that when the second object was oriented straight participants completed the grasping action significantly faster (p = 0.02) when grasping the larger cylinder (M = 0.68 seconds, SE = 0.05) relative to the smaller cylinder (M = 0.66 seconds, SE = 0.06). No main effect of size of the first object F (1, 14) = 1.65, p = 0.23, η_p^2 = 0.13, size of the second object, F (2, 28) = 0.98, p = 0.39, η_p^2 = 0.08, and orientation of the second object, F (2, 28) = 1.61, p = 0.22, η_p^2 = 0.13.

3.3.5 Time to Peak Grip Aperture

No significant interaction was found for size of the first object, size of the second object and orientation of second object, F (4, 56) = 1.01, p = 0.41, η_p^2 = 0.08. No significant interaction between size of first object and size second object, F (2, 28) = 0.39, p = 0.68, η_p^2= 0.03, size of first object and orientation of second object, F (2, 28) = 2.55, p = 0.12, η_p^2= 0.18, and size of second object and orientation of second object, F (4,56) = 1.25, p = 0.3, η_p^2 = 0.1. There was a main effect of size of the first object, F (1, 14) = 13.64, p = 0.004, η_p^2 = 0.55. Specifically, participants time to PGA was faster for the smaller cylinder (M = 0.53 seconds, SE = 0.003) relative to the larger cylinder (M = 0.55 seconds , SE= 0.003). No main effect was found for the size of the second object, F (2, 28) = 0.25, p =0.78, η_p^2 = 0.02, and orientation of second object, F (2, 28) = 0.68, p = 0.52, η_p^2 = 0.06.

3.4 Discussion

The main purpose of this experiment was to see whether we would obtain the same results as our previous study (see chapter 2) even though no action was required for the second segment of the sequence. Specifically, participants performed a grasping action towards a cylinder (the first object) placed it on its target location and then identified the next object by verbally describing its size (relative to the first object) and its orientation. Once again, our results revealed that participants reached out to grasp the cylinder with a significantly smaller PGA when the second object was smaller relative to when it was the same size or larger than the cylinder's diameter. However, the orientation of the second object had no effect on the grip orientation used to grasp the cylinder.

Since we found the same interference effect when there is only one action to be performed as opposed to two actions, it strongly suggests that the interference effects described in previous studies could have emerged via attentional mechanisms. After all, the fact we found any interference effect with this experiment (e.g., only one action to be performed) contradicts the holistic planning hypothesis proposed by others (Haggard, 1998, Hesse and Deubel, 2010;

Seegelke et al., 2012, 2013). We are once again finding this unique result in which an interference effect only happens when the second object is smaller. In our previous study, we argued this could be explained by the fact that when the second object is smaller relative to the first object this will require more motor planning/online processing, and this causes interference when programming the first action. However, in the case of this experiment, we cannot attribute the interference effect to this explanation since there was no action to be planned/performed towards the second object.

We also did not find the typical interference effect you would expect when incorporating a perceptual task (e.g., allocentric coding mechanisms of the ventral stream causing size contrast effect between first and second object; Ganel & Goodale, 2003; Goodale & Humphrey, 1998). Thus, our results suggest that we are capturing the same interference effect regardless of whether participants are performing an action or performing a perceptual judgment task with the second object of the sequence; and the nature of the effect seems to be driven by the true size representation of the second object. One possible explanation could be that participants are deploying attention towards the second object prior and/or during the first movement (Baldaulf, Wolf, & Deubel, 2006; Baldauf, Cui, & Andersen, 2008), and this causes the automatic encoding of its associated motor prototype (Chao & Martin, 2000; Grèzes et al., 2003, Murata et al., 1997, Rice et al., 2007, Tucker & Ellis, 1998, 2001; Valyear et al., 2007) which then competes with the motor planning of the first action and causes interference (Cisek and Kalaska 2005, 2010; Chapman et al. 2010, 2014, Gallivan et al., 2015, 2016; Klaes et al. 2011; Stewart et al., 2013, 2014, Tipper et al., 1998, Wood et al., 2011) regardless of whether its driven by attention-for-action or attention-for-perception (Hommel, 2009; Kikumoto & Mayr, 2020; Takacs et al., 2020). More specifically, since participants needed to actively pay attention to the size of the first object it could have specifically facilitated the size processing of the second object. Thus, the interference effect could be driven by the competition between the two different sizes required for both action plans that are activated in parallel (even during perception the action plan is automatically elicited). However, since orientation was only a feature of the second object there is no competition between action plans, so no effects based on orientation when executing the first action. Although this explanation makes theoretical sense, it does not explain why we are only finding an interference effect for when the second object is smaller and not larger.

One possible reason could be that when the first object is larger, the tuning of the participants' aperture (the gradual opening between the index and thumb until it reaches its PGA) will overlap with the PGA associated with the smaller second object. However, when the first object is smaller it will not overlap with the PGA associated with the larger second object since it will reach its own required PGA before that point, and this potentially makes it easier for the motor system to inhibit the interference from that action. Therefore, this could be the reason why the smaller object is causing interference consistent with its own size and not the larger object. One simple way that this hypothesis could be further explored is by having participants start with their fingers stretched apart instead of having their fingers pinched together. In that case, we should see the opposite size effect: participants should grasp towards the first object with a significantly larger PGA when the second object is larger but no effect for when the second object is smaller.

Based on this current study and our previous study (see chapter 2), it seems that the orientation effects found in Hesse and Deubel's (2010) study must have been facilitated by the fact that the first action was always the same object and that participants were not fully engaging the online visuomotor mechanisms of the dorsal stream's grasping circuit. More specifically, it seems that when measuring an action that is fully guided under full online control (via changing its size on a random basis), the orientation feature of the second object does not get incorporated into the first action. However, we still cannot rule out the fact that it is possible that that participants are not actively processing the orientation of the second object in advance of the first action, since they are preoccupied with size processing because of our size manipulations, and that is why we are not finding any orientation effects.

One way to further investigate this would be to use the same paradigm as our first experiment but with the crucial modification of occluding vision for the second action. Participants would indeed have full-vision when performing the first action but after they would lose vision (via LCD glasses turning opaque) so participants would perform a memory-guided action for the second sequence. This would ensure that participants are indeed fully processing all the relevant features (e.g., size and orientation) of the second object prior to performing the first action. In this case, would we continue to see the first action being resistant (as a default mechanisms of the online control system) to any orientation effects or would we finally see similar results as Hesse and Deubel (2010)? This would allow us to further conclude what exact mechanisms are driving the similar results obtained in this current experiment and our previous experiment.

To summarize, we modified our current experiment so that participants did not perform any action towards the second object, instead a perceptual judgment was performed, to see whether our previous findings (chapter 2) were driven by mechanisms of motor planning or by mechanisms of attentional control. The fact we found the same unique result, in which participants reached out for the first object with significantly smaller PGA when the second object was smaller relative to the same size or larger, strongly suggest that this particular interference effect is driven by attentional capture mechanisms that implicitly activate motor representations, and not by future motor planning strategizing. Moreover, based on these and our previous results, we have found no evidence in favour of the holistic planning hypothesis proposed by previous research (Haggard, 1998; Hesse & Deubel, 2010; Seegelke et al., 2012, 2013).

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CHAPTER 4: INTERACTIONS BETWEEN SEQUENTIAL ACTIONS: EXPLORING THE EFFECTS OF CLOSED-LOOP AND OPEN-LOOP CONDITIONS

4.1 Introduction

It has been well demonstrated that when planning a grasping action, the anticipation of the future task demands has a direct influence on the way the movement is executed (Ansuini et., 2008; Armbrüster & Spijkers, 2006; Cohen & Rosenbaum, 2004; Gentilucci et al., 1997; Haggard, 1998; Johnson-Frey et al., 2004; Marteniuk et al., 1987; Rosenbaum et al., 1992, 1996). However, these results were demonstrated when performing an action on a single object and measuring the effects of action intentions and/or subsequent action with the very same object. Although these studies showed strong evidence that the brain utilizes advance planning mechanisms in which movement sequences are planned holistically in the context of performing a single grasp, the question remains whether this can be shown with a sequence involving multiple objects. Essentially, can a future grasping action performed on a different object influence how a current action is performed on another object.

To explore this exact question, Hesse and Deubel (2010) designed a study in which participants needed to first grasp a cylinder, place it within a target area (e.g., outlined circle), then grasp a bar that was either oriented towards the left, straight, or right. In their first experiment they altered the diameter of the target area for the cylinder to see whether there was a difference when the first action is considered more easy (larger diameter) or harder (smaller diameter). The results revealed that participants' grip orientation when grasping the cylinder was influenced by the orientation of the second object for both the easy and hard conditions (e.g., second object oriented to the left made participants significantly use a more leftward grip orientation when grasping the first object). In a second experiment, Hesse and Deubel (2010) made the first action more difficult by making the participants place the cylinder on a short pin that was mounted in the center of the target area. As a result, the first action was no longer influenced by the second object. It was therefore concluded that when the first action has a low level of difficulty, separate movement sequences will be planned holistically in which features of the second object will be implemented within the first movement to optimize the movement end-goal (e.g., grip orientation already pre-adjusted to perform the final action as the first action takes place).

However, we also know that visual attention is deployed across all action relevant locations (e.g., attentional landscape) when planning sequential movements (Baldaulf, Wolf, & Deubel, 2006; Baldauf, Cui, & Andersen, 2008) and that merely paying attention to an object is sufficient to cause the automatic encoding of its associated motor prototype (Chao & Martin, 2000; Grèzes et al., 2003, Murata et al., 1997, Rice et al., 2006, Tucker & Ellis, 1998; Valyear et al., 2006). Thus, it remains possible that the results reported by Hesse and Deubel (2010) was driven by an attentional interference effect and not because of advance motor planning mechanisms (e.g., holistic planning hypothesis). To achieve a better understanding of the neural mechanisms at play when planning sequential grasping actions, we conducted two studies using Hesse and Deubel's paradigm but with the addition of the crucial modifications of adding two possible sizes for the first object and adding three possible sizes for the second object.

The reason we added two possible sizes to the first object was to ensure that participants were indeed relying on real-time visuomotor control mechanisms when grasping the first object. Previous studies looking at sequential effects (Haggard, 1998; Hesse & Deubel, 2010, LeBlanc & Westwood, 2016; Seegelke et al., 2012, 2013, 2015) always used the same first object throughout their experiment. This led to the criticism that perhaps these effects were driven by the fact that participants were not required to fully engage real-time visuomotor mechanisms (e.g., fully relying on the grasping circuit of the dorsal stream) towards the first object since they always knew what to expect, and this facilitated the action to rely on memory mechanisms of the ventral stream (Westwood & Goodale, 2003; Singhal et al., 2013): a potentially more vulnerable route for interference. To avoid this question, we randomized the size of the cylinder on a trial-by-trial basis to ensure full visuomotor mechanisms were being utilized during the act of the first grasp.

In addition to randomizing the orientation of the second object, we also randomized the size of the second object between three possible sizes: smaller than the cylinder's diameter, the same size, or larger. We argued that if the holistic planning hypothesis is true the first action should only be influenced by the orientation of the second object and not its size. Grasping a cylinder can afford to be grasped by any type of grip orientation, so incorporating the orientation of the second action into the first action could better serve the final action without impairing the first action. However, incorporating the size of the second object into the first movement serves no strategic advantage to the overall end-goal since the actor's hand aperture must always close to the size of the first object before grasping the second one. In contrast, if the attentional interference hypothesis is true, all action relevant features (e.g., size and orientation) could interfere with the kinematics of the first action since the interference is driven via an accidental effect, (i.e., visual selective mechanisms implicitly activating the future motor plan in parallel with the current motor plan), not a strategic effect.

The first experiment we conducted required participants to perform two sequential grasping actions (like Hesse and Deubel's study) and our second experiment required participant to grasp the first object and then perform a perceptual judgement task about the second object. In both of our studies, we found a similar interference effect: when the second object was smaller than the cylinder, participants reached out with a smaller PGA when grasping the cylinder (see chapters 2 and 3). However, in both of our experiments we never found any orientation effects as reported by Hesse and Deubel (2010). Based on these results, it seems when participants are required to engage in real-time visuomotor control for the first action it becomes immune to the influence of the second object's orientation, which does not support the holistic planning hypothesis. In contrast, the fact that a particular size effect was found when either performing a second action or performing a perceptual judgment (no action required), strongly suggest that this specific effect is driven by attentional mechanisms triggering implicit motor processes and not some form of higher-order motor planning.

Based on similar findings across both of our previous studies, we hypothesized that the size effect we are finding is most likely driven by the competition between the two different sizes required for both action plans that are activated in parallel (Cisek and Kalaska 2005, 2010; Chapman et al. 2010, Gallivan et al., 2015, 2016; Klaes et al. 2011; Stewart et al., 2013, 2014, Tipper et al., 1998, Wood et al., 2011). Since orientation was only a feature of the second object, there is no other orientation feature present to compete with and as a result the first action is not affected by the second object's orientation. This explanation lays out a reasonable theoretical foundation to explain the meaning of these results, but one caveat is the fact that we are only finding a size effect with the smaller object and not the larger object. A hypothesis was proposed based on the way aperture tuning develops throughout the movement before achieving PGA as to why this only happens for the smaller second object and not the larger object in relation to the positioning of the fingers at the start location (see section 3.4 for a more elaborate explanation and future experiment proposal). Despite that being worth further investigating, we believe it is first necessary to control a factor that we did not control for during our previous experiments to provide more clarity to our results and Hesse and Deubel's (2010) results.

Specifically, we still cannot rule out the fact that it is possible that that participants are not actively processing the orientation of the second object in advance of the first action, since they are preoccupied with size processing because of our size manipulations, and that is why we are not finding any orientation effects. Therefore, for this experiment we want to use the similar paradigm as our first study (see chapter 2) but have a condition where the participants will be essentially forced to deploy attention to the second object's orientation prior to executing the first action. This will be done by occluding participants vision after the completion of the first action. By engaging participants in an open-loop condition (i.e., memory-guided) for the second action, it will ensure that they will deploy attention towards the second object prior to initiating the first movement; this is their only chance to visually process the action-relevant features of the second object since they won't be able to rely on vision once the first movement is completed.

This open-loop condition will allow us to measure the first action with certainty that the participants did indeed pay attention to the orientation (and size) of the second object prior to initiating the movement. We will be curious to see if we can finally reveal the same orientation effects shown in Hesse and Deubel's (2010) experiment. If so, this will confirm that our previous results were most likely driven by the modification we made to their paradigm that favoured size processing and this overshadowed the orientation feature of the second object, hence why we found some evidence for size interference but no evidence for orientation interference. If we still find no orientation effect under this condition, this suggests that when performing an action, guided by real-time visuomotor control, the features of the second object do not interfere (or strategically influence) with the first movement unless there is two competing features that overlap in action plans – as we previously found, a smaller second object will interfere with the programming of the PGA of the first action but not a larger second object (e.g., tuning the aperture towards the larger first object will require the movement of the fingers to pass through the PGA required for the smaller second object, but this not the case if the second object is larger).

We will also implement a closed-loop condition (full vision during second action) to see if we can yet again replicate the unique size effect found in our previous two experiments. Therefore, participants will complete two different blocks of trials. One block will require them to perform the second action under closed-loop condition (vision will not be occluded at any point during the movement sequence) and the other block will be under open-loop condition (vision will be occluded after completing the first action). The type of block that the experiment will start/finish with will be counterbalanced across participants. Like our previous experiments, two possible sizes will be randomized for the first object (cylinder) and the second object will be randomized between three possible sizes (larger, smaller, or same size as diameter of the cylinder) and three possible orientations (tilted 45 degrees to the right or left, and straight). We will analyze each block of trials separately to see if the first grasping action was affected by the size and/or orientation feature of the second object. We hope that the addition of the open-loop condition will help us address some unsolved explanations regarding our own previous results relative to previous findings (Haggard, 1998; Hesse & Deubel, 2010; Seegelke et al., 2012, 2013).

4.2 Methods

4.2.1 Participants

Fifteen undergraduate students at Dalhousie University participated in the current study in exchange for partial course credit. All were right-handed, had normal to corrected-to-normal vision, and no history of neurological deficit as ascertained by self-report. Each participant provided informed written consent prior to participation in accordance with guidelines established by the Dalhousie University Research Ethics Board.

4.2.2 Materials

Same materials and set-up as our previous experiment (see section 2.2.2 and Figure 1)

4.2.3 Procedure

The procedure for the first action was the same as our previous first experiment, as well as the general experimental setup (see section 2.2.3 and Figure 1). However, in this experiment participants performed two blocks of trials in which the second action was performed under different visual conditions for each block. The closed-loop condition was no different than our previous first experiment, participants had full vision and were required to reach out and grasp the second object once the first action was completed. In the open-loop condition, participants' vision is occluded (via LCD glasses) 500ms after movement onset, thus leaving the participants to perform a memory-guided action for the second action. The order in which block the participants start/finish with was counterbalanced across participants (e.g., 7 participants started with the open-loop condition and 8 participants started with the closed-loop condition). Each participant performed a total of 72 trials (36 trials for each type of cylinder and four trials for each possible size and orientation combinations) for each type of block, leading to a total of 144 trials.

4.2.4 Data Processing

Data collection and processing followed the same procedures as our first experiment (see section 2.2.4), but in this case we first performed a 2 (size of cylinder) x 3 (size of second object) x 3 (orientation of second object) x 2 (condition type) repeated measures ANOVA. Based on the nature of our hypothesis, we also performed a separate 2 (size of cylinder) x 3 (size of second object) x 3 (orientation of second object) repeated measures ANOVA for each type of condition to directly compare our current results with previous results. Post hoc analysis was done with Bonferroni-corrected t tests.

4.3 Results

4.3.1 Peak Grip Aperture

The results showed no significant interaction between the size of the cylinder's diameter (first object), size of rectangular object (second object), orientation of the rectangular object (second object), and type of condition, F (4, 56) = 1.08, p = 0.37, $\eta_p^2 = 0.09$; and no significant interaction was found when breaking down all other possible interactions ($p > 0.05$). A main effect for size of the cylinder was found, F (1, 14) = 53.04 $p < 0.001$, $\eta_p^2 = 0.82$ in which participants reached out with a larger PGA for the larger cylinder (M = 77.6 mm, SE = 0.17) than the smaller cylinder (M = 73.88, SE = 0.15). There was no main effect of size of the second object, F (2,28) = 0.24, p=0.79, η_p^2= 0.02, no main effect of orientation of the second object, F (2,28) = 0.33, p=0.73, η_p^2= 0.03 and no main effect of condition F (1,14) = 1.26, p=0.29, η_p^2= 0.1.

4.3.1.2 Closed-Loop Condition

The results showed no significant interaction between the size of the cylinder's diameter (first object), size of rectangular object (second object), and orientation of the rectangular object (second object), F (4, 56) = 0.51, p = 0.73, $\eta_p^2 = 0.05$. There was also no significant interaction between the size of the first object and size of the second object, F (2, 28) = 0.92, p = 0.91, $\eta_p^2 = 0.08$; the size of the first object and orientation of second object, F (2, 28) = 1.39, p = 027, $\eta_p^2 = 0.11$; the size of the second object and the orientation of the second object, F (4, 56) = 0.39, p = 0.81, $\eta_p^2 = 0.03$. As expected, there was a main effect for size of the first object, F (1, 14) = 42.33, $p < 0.001$, $\eta_p^2 = 0.88$. Participants reached out with a larger PGA for the larger cylinder (M = 77.3 mm, SE = 0.17) than the smaller cylinder (M = 73.23, SE = 0.16). A main effect of size for the second object was also found, F (2, 28) = 3.36, p = 0.049, $\eta_p^2 = 0.23$. Post-hoc analysis (Bonferroni correction) revealed a significant difference between the smaller second object in comparison to the larger size (p=0.04) but no difference between the smaller size and the same size (p=0.13) and no difference between the same size and the larger size (p=0.41). As seen in Figure 6, participants reached out for the first object with a smaller peak grip aperture when the second object was smaller than the first one (M= 74.89mm, SE= 0.19) relative to if the second object was larger (M=75.53mm, SE=0.21). No main effect of orientation of the second object was found, F (2,28) = 0.85, p=0.44, $\eta_p^2 = 0.07$.

4.3.1.2 Open-Loop Condition

The results showed no significant interaction between the size of the cylinder's diameter (first object), size of rectangular object (second object), and orientation of the rectangular object (second object), F (4, 56) = 1.32, p = 0.28, $\eta_p^2 = 0.1$. There was also no significant interaction between the size of the first object and size of the second object, F (2, 28) = 0.91, p = 0.91, $\eta_p^2 = 0.08$; the size of the first object and orientation of second object, F (2, 28) = 0.21, p = 0.82, $\eta_p^2 = 0.18$; the size of the second object and the orientation of the second object, F (4, 56) = 0.06, p = 0.99, $\eta_p^2 = 0.06$. As expected, there was a main effect for size of the first object, F (1, 14) = 38.45, $p < 0.001$, $\eta_p^2 = 0.78$. Participants reached out with a larger PGA for the larger cylinder (M = 78.05 mm, SE = 0.18) than the smaller cylinder (M = 74.54, SE = 0.18). No main effect of size of the second object was found, F (2,28) = 0.55, p=0.59, $\eta_p^2 = 0.05$, as seen in Figure 6 and no main effect of orientation of the second object was found, F (2,28) = 0.79, p=0.46, $\eta_p^2 = 0.07$.

4.3.2 Grip Orientation

The results showed no significant interaction between the size of the cylinder's diameter (first object), size of rectangular object (second object), orientation of the rectangular object (second object), and type of condition, F (4, 56) = 1.53, p = 0.21, η_p^2 = 0.12; and no significant interaction was found when breaking down all other possible interactions (p > 0.05). There was no main effect for size of cylinder, F (1, 14) = 0.72, p = 0.41, η_p^2 = 0.06, size of second object, F (2,28) = 0.24, p=0.79, η_p^2= 0.02, orientation of the second object, F (2,28) = 0.33, p=0.73, η_p^2= 0.03, and condition, F (1, 14) = 0.001, p = 0.99, η_p^2 = 0.001.

4.3.2.1 Closed-Loop Condition

No significant interaction was found between size of first object, size of second object and orientation of second object, F (4,56) = 0.81, p= 0.53, η_p^2 = 0.07. There was also no significant interaction between size of first object and size of second object, F (2, 1) = 1.02, p =0.38, η_p^2= 0.08, size of first object and orientation of second object, F (2, 28) = 0.44, p= 0.65, η_p^2= 0.04 and size of second object and orientation of second object, F (4, 56) = 1.08, p=0.37, η_p^2= 0.09. No main effect of size of the first object, F (1, 14) = 0.01, p = 0.98, η_p^2 = 0.001; size of the second object, F (2, 28) = 0.17, p = 0.85, η_p^2 = 0.02; and no main effect of orientation of the second object, F (2,28) = 0.05, p = 0.95, η_p^2 = 0.01 as seen in Figure 7.

4.3.2.2 Open-Loop Condition

No significant interaction was found between size of first object, size of second object and orientation of second object, F (4,56) = 0.87, p= 0.49, η_p^2 = 0.07. There was also no significant interaction between size of first object and size of second object, F (2, 28) = 0.01, p =0.99, η_p^2= 0.001, size of first object and orientation of second object, F (2, 28) = 2.99, p= 0.07, η_p^2= 0.21 and size of second object and orientation of second object, F (4, 56) = 0.29, p=0.89, η_p^2= 0.03. No main effect of size of the first object, F (1, 14) = 1.84, p = 0.2, η_p^2 = 0.14; no main effect for the size of the second object, F (1.31, 18.35) = 2.95, p = 0.09, η_p^2 = 0.21. There was also no main effect of orientation F (1.33, 18.66) = 3.25, p = 0.08, $\eta_p^2 = 0.22$; however, as seen in Figure 7, the results are trending in the direction of what Hesse and Deubel (2010) reported albeit not even close to the same magnitude.

4.3.3 Reaction Time

The results showed no significant interaction between the size of the cylinder's diameter (first object), size of rectangular object (second object), orientation of the rectangular object (second object), and type of condition, F (4, 56) = 0.89, p = 0.47, $\eta_p^2 = 0.07$; No significant interaction was found when breaking down all other possible interactions ($p > 0.05$) except for the interaction between cylinder size and type of condition, F (1, 14) = 7.36, p = 0.02, $\eta_p^2 = 0.4$. It was shown that when grasping the smaller cylinder participants were significantly (p= 0.01) faster to initiate the first action during the closed-loop condition (M= 0.49 seconds SE = 8.3) relative to the open-loop condition (M= 0.53 seconds, SE= 7.6) but there was no difference between conditions when grasping the larger cylinder (p=0.45). There was no main effect of cylinder size, F (1, 14) = 0.01, p = 0.94, $\eta_p^2 = 0.001$, size of second object, F (2, 28) = 0.76, p = 0.48, $\eta_p^2 = 0.06$, orientation of second object, F (2, 28) = 0.07, p = 0.94, $\eta_p^2 = 0.05$, and type of condition F (1, 14) = 0.37, p = 0.55, $\eta_p^2 = 0.03$.

4.3.3.1 Closed-Loop Condition

No significant interaction was found between size of first object, size of second object and orientation of second object, F (4,56) = 2.53, p= 0.09, $\eta_p^2 = 0.18$. There was also no significant interaction between size of first object and size of second object, F (2, 28) = 2.05, p =0.15, $\eta_p^2 = 0.15$, size of first object and orientation of second object, F (2, 28) = 1.04, p= 0.37,

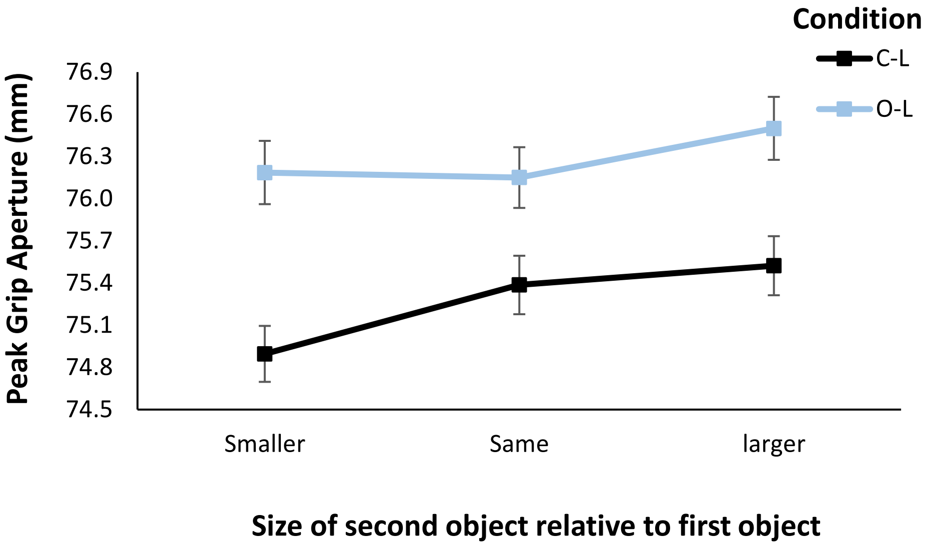

Figure 6. Mean peak grip aperture when performing a grasping action to the first object in relation to the size of the second object. The closed-loop condition (full-vision for second action) is depicted in black and the open-loop condition (memory-guided for second action) in blue. Error bars indicate SEM. As shown, in the closed-loop condition PGA for the first action is significantly smaller when the second object is smaller relative to when the second object is larger than the first object. However, no significant difference between size of second object for the open-loop condition.

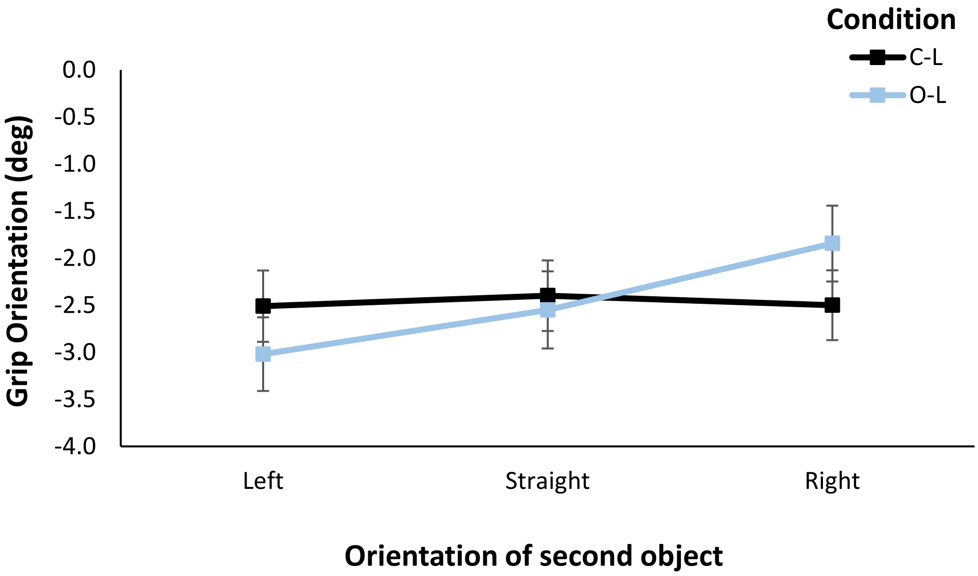

Figure 7. Mean grip orientation when performing a grasping action to the first object in relation to the orientation of the second object. The closed-loop condition (full-vision for second action) is depicted in black and the open-loop condition (memory-guided for second action) in blue. Error bars indicate SEM. No significant differences were found for either condition.

η_p^2= 0.09 and size of second object and orientation of second object, F (4, 56) = 1.68, p=0.17, η_p^2= 0.13.No main effect of size of the first object, F (1, 14) = 3.28, p = 0.10, η_p^2 = 0.23; size of the second object, F (2, 28) = 0.13, p = 0.88, η_p^2 = 0.01; and no main effect of orientation of the second object, F (2,28) = 1.03, p = 0.37 η_p^2 = 0.08.

4.3.3.2 Open-Loop Condition

No significant interaction was found between size of first object, size of second object and orientation of second object, F (4,56) = 0.46, p= 0.76, η_p^2 = 0.04. There was also no significant interaction between size of first object and size of second object, F (2, 28) = 0.56, p =0.58, η_p^2= 0.05, size of first object and orientation of second object, F (2, 28) = 0.28, p= 0.76, η_p^2= 0.02 and size of second object and orientation of second object, F (4, 56) = 0.63, p=0.64, η_p^2= 0.05. No main effect of size of the first object, F (1, 14) = 1.02, p = 0.34, η_p^2 = 0.08, size of the second object, F (2, 28) = 0.7, p = 0.5, η_p^2 = 0.06, and orientation of second object, F (2, 28) = 0.66, p = 0.53, η_p^2 = 0.06.

4.3.4 Movement Time

No significant interaction was found for the size of the first object, size of the second object, orientation of the second object, and type of condition, F (4, 56) = 1.17, p = 0.34, η_p^2 = 0.09. No significant interaction was found when breaking down all other possible interactions (p > 0.05) except for the interaction between cylinder size and orientation of the second object, F (2, 28) = 5.4, p = 0.01, η_p^2 = 0.33. It was shown that when grasping the smaller cylinder participants were significantly faster (p= 0.04) when the second object was oriented to the right (M= 0.426 SE = 0.004) relative to the left (M= 0.436, SE = 0.005) but this same comparison was not significant (p= 0.3) when grasping the larger cylinder. There was no main effect of cylinder size, F (1, 14) = 0.84, p = 0.38, η_p^2 = 0.07, size of second object, F (2, 28) = 0.15, p = 0.85, η_p^2 =

0.01, orientation of second object, F (2, 28) = 0.79, p = 0.46, $\eta_p^2 = 0.07$, and type of condition F (1, 14) = 2.65, p = 0.13, $\eta_p^2 = 0.19$.

4.3.4.1 Closed-Loop Condition

No significant interaction was found between size of first object, size of second object and orientation of second object, F (4,56) = 2.6, p= 0.08, $\eta_p^2 = 0.19$. There was also no significant interaction between size of first object and size of second object, F (2, 28) = 0.61, p =0.55, $\eta_p^2= 0.05$, and size of second object and orientation of second object, F (4, 56) = 0.8, p=0.53, $\eta_p^2= 0.07$. However, there was a significant interaction between size of the first object and orientation of second object, F (2, 28) = 5.13, p = 0.02, $\eta_p^2= 0.32$. Specifically, participants were significantly faster at completing the first action when grasping the small cylinder (M=0.433, SE= 0.004) relative to the larger cylinder (M=0.453, SE=0.004) when the second object was oriented towards the right (p= 0.01). There was no main effect of size of the first object, F (1, 14) = 0.93, p = 0.36, $\eta_p^2 = 0.08$, size of the second object, F (2, 28) = 0.34, p = 0.72, $\eta_p^2 = 0.03$, and no main effect of orientation of the second object, F (2,28) = 1.57, p = 0.23 $\eta_p^2 = 0.12$.

4.3.4.2 Open-Loop Condition

No significant interaction was found between size of first object, size of second object and orientation of second object, F (4,56) = 0.2, p= 0.94, $\eta_p^2 = 0.02$. There was also no significant interaction between size of first object and size of second object, F (2, 28) = 0.18, p =0.84, $\eta_p^2= 0.02$, size of first object and orientation of second object, F (2, 28) = 0.88, p= 0.43, $\eta_p^2= 0.07$, and size of second object and orientation of second object, F (4, 56) = 0.97, p=0.43, $\eta_p^2= 0.08$. No main effect of size of the first object, F (1, 14) = 0.1, p = 0.76, $\eta_p^2 = 0.01$, size of the second object, F (2, 28) = 0.29, $p = 0.75$, $\eta_p^2 = 0.03$, and orientation of second object, F (2, 28) = 0.63, $p = 0.54$, $\eta_p^2 = 0.05$.

4.3.5 Time to Peak Grip Aperture

The results showed no significant interaction between the size of the cylinder's diameter (first object), size of rectangular object (second object), orientation of the rectangular object (second object), and type of condition, F (4, 56) = 2.1, $p = 0.09$, $\eta_p^2 = 0.12$. No significant interaction was found when breaking down all other possible interactions ($p > 0.05$). There was no main effect for size of cylinder, F (1, 14) = 0.72, $p = 0.41$, $\eta_p^2 = 0.06$, size of second object, F (2,28) = 0.24, $p=0.79$, $\eta_p^2= 0.02$, and orientation of the second object, F (2,28) = 0.33, $p=0.73$, $\eta_p^2= 0.03$. However, there was a main effect for the type of condition, F (1,14) = 24.22, $p= 0.001$, $\eta_p^2= 0.69$. When participants performed the open-loop trials (M= 0.234 seconds, SE = 0.003, they attained peak grip aperture significantly faster relative to the closed-loop trials (M = 0.268 seconds, SE = 0.002).

4.3.5.1 Closed-Loop Condition

No significant interaction was found between size of first object, size of second object and orientation of second object, F (4,56) = 2.1, $p= 0.09$, $\eta_p^2 = 0.19$. There was also no significant interaction between size of first object and size of second object, F (2, 28) = 0.92, $p =0.41$, $\eta_p^2= 0.08$, and size of second object and orientation of second object, F (4, 56) = 0.77, $p=0.55$, $\eta_p^2= 0.06$. However, there was a significant interaction between size of first object and orientation of second object, F (2, 28) = 4.78, $p= 0.02$, $\eta_p^2= 0.3$. When grasping the smaller cylinder participants were quicker to attain PGA (M=0.262 seconds, SE = 0.002) relative to grasping the larger cylinder (M= 0.280 seconds, SE= 0.002) when the second object was oriented towards the right ($p =0.03$) but not when it was oriented towards the left ($p=0.13$) or placed straight ($p=0.89$). No main effect of size of the first object, F (1, 14) = 0.06, $p = 0.82$, $\eta_p^2 = 0.01$, size of the second object, F (2, 28) = 0.16, p = 0.85, $\eta_p^2 = 0.01$, and orientation of second object, F (2, 28) = 1.43, p = 0.26, $\eta_p^2 = 0.12$.

4.3.5.2 Open-Loop Condition

No significant interaction was found between size of first object, size of second object and orientation of second object, F (4,56) = 1.03, p= 0.4, $\eta_p^2 = 0.09$. There was also no significant interaction between size of first object and size of second object, F (2, 28) = 0.76, p =0.48, η_p^2= 0.07, size of first object and orientation of second object, F (2, 28) = 0.48, p= 0.62, η_p^2= 0.04, and size of second object and orientation of second object, F (4, 56) = 1.05, p=0.39, η_p^2= 0.09. No main effect of size of the first object, F (1, 14) = 2.07, p = 0.18, $\eta_p^2 = 0.16$, size of the second object, F (2, 28) = 2.51, p = 0.11, $\eta_p^2 = 0.19$, and orientation of second object, F (2, 28) = 0.76, p = 0.48, $\eta_p^2 = 0.07$.

4.4 Discussion

This experiment was designed to ensure participants were deploying attention towards the features of the second object prior to initiating the first grasping action. We previously failed to find any orientation effect (chapter 2 and 3) as reported by Hesse and Deubel (2010). However, because we applied crucial modifications to their paradigm, it is possible that we overshadowed the orientation feature of the second object by randomizing the size of the first and second object on a trial-by-trial basis. Thus, to ensure participants deployed attention to the orientation feature of the second object before starting the action sequence, we had a condition (open-loop condition) where participants' vision was occluded after completing the first act of grasping the cylinder. This 'forced' the participants to visually process the second object prior to starting the first movement, since this was their only opportunity to store in memory the action relevant features (e.g., orientation and size) needed to successfully guide the second grasping action. In addition, we also had another condition (e.g., closed-loop condition) where participants performed the full action sequence with vision (same paradigm as Chapter 2). This allowed us to make a direct comparison between the different conditions and to further explore whether we can replicate our own previous results.

For the closed-loop condition, our results once again revealed no significant effect of the second object's orientation on the grip orientation used to grasp the cylinder. Surprisingly, this was also the case for the open-loop condition. However, the results in the open-loop condition were indeed trending in the direction (see Figure 7) that Hesse and Deubel (2010) reported - unlike our previous experiments (see Figures 3 and 5). Nevertheless, our results are not close to the same magnitude. They reported over a 10-degree difference in grip orientation between the left vs. right orientation whereas we are only seeing a 1-degree difference. This further confirms that when participants are fully engaging in real-time visuomotor control for the first action, the orientation of the second object does not influence the grip orientation used to pick up the cylinder (as seen in Chapter 2 and 3). This also reveals that the orientation feature of the second action can be held in memory without significantly affecting how the first action is programmed since participants could still successfully perform the second action. Based on these results, we once again do not provide any evidence in favour of the holistic planning hypothesis proposed by previous research (Haggard, 1998; Hesse & Deubel, 2010; Seegelke et al., 2012, 2013).

However, for the closed-loop condition we yet again found a significant difference in PGA relative to the size of the second object. Specifically, participants were grasping the cylinder with a smaller PGA when the second object was smaller relative to if it was larger (see Figure 6). This is a similar finding as our previous results (see Figure 2 & 4) albeit in this case there was no difference between the smaller object and the same size object. Nevertheless, this result still favours the view that the size effect we are finding across our experiments is most likely an artifact caused by the competition between the two different sizes required for both action plans that are activated in parallel (Cisek and Kalaska 2005, 2010; Chapman et al. 2010, 2014, Gallivan et al., 2015, 2016; Klaes et al. 2011; Stewart et al., 2013, 2014, Tipper et al., 1998, Wood et al., 2011). Specifically, because participants are starting the movement with their fingers pinched together, the size representation of the smaller second object will overlap with the size representation of the larger cylinder: tuning the aperture towards the larger first object will require the movement to pass through the PGA required for the smaller second object, but this not the case when the second object is larger than the cylinder.

Nonetheless, no size effect was revealed in the open-loop condition. This is a bit surprising since we thought that a greater amount of attention should be deployed towards the second object within this condition, so the features of the second object should have a greater chance of interfering with the first grasping action. However, it is important to note that we are now forcing the participants to program a memory-guided action for the second object, and this will of course heavily rely on ventral stream processing (Cohen, et al., 2009; Gentilluci et al., 1996, Hu & Goodale, 2000; Rossetti, 1998, Singhal et al. 2013; Westwood et al., 2000; Westwood & Goodale, 2003). The features of the second object are likely held in memory as a perceptual trace that will later guide the following action. Therefore, the act of actively storing the features in memory outside of the grasping circuit could simultaneously make the first action more immune to its interferences – unlike planning another action fully guided by real-time visuomotor control (closed-loop condition and Chapter 2 results) which potentially causes a competition between action plans in which overlapping features can interfere.

This explanation might sound incompatible with the fact we found a size effect even when participants are performing a perceptual task for the second object (chapter 3), but it is important to note in that experiment the perceptual task did not rely on memory mechanisms. Specifically, the implicit activation of the size representation of the second object was not actively stored, via its perceptual trace, as a separate action. So, when the size overlapped with the PGA requirements of the first grasp it caused interference in similar fashion as seen when planning two visually guided sequential grasping actions. In addition, the perceptual task required participants to make a direct size comparison with the first object whereas this was not the case for the open-loop condition. Thus, the nature of the perceptual task perhaps accommodated a size interference to emerge whereas the open-loop condition potentially did the opposite by actively treating the sequence as two distinct segments. Based on the one-target advantage literature (Adam et al., 2000, 2001; Bested et al., 2018; Helsen et al., 2001; Khan et al., 2006, 2008, 2010, Mottram et al., 2014, Rand et al., 1997, 2000), if it is indeed the case that the open-loop condition is causing the sequence to be divided into separate distinct actions based on their distinct modes of operation, there should be some type of evidence that shows the participants are either initiating or approaching the first action in a faster way than the closed-loop condition. It was found that participants time to attain PGA was indeed faster in the open-loop condition relative to the close-loop condition, but no such evidence was found when looking at the RT and MT results. Therefore, it remains questionable if that is the proper explanation for the lack of a size interference (and potentially orientation effect) in the open-loop condition.

The main purpose of this experiment was to ensure participants deployed attention to the action-relevant features of the second object prior to initiating the first action. Specifically, since our previous findings showed no orientation effects, we wanted to rule out the possibility that participants were simply not paying attention to the orientation of the second object in advance. Despite the manipulation of adding an open-loop condition, the orientation of the second object still did not significantly influence the grip orientation used to grasp the first object. The fact that we cannot get anywhere near the same effects as Hesse and Deubel (2010) suggest that their results must be driven by the fact that the first object is always the same size and not guided under real-time visuomotor mechanisms. It seems that since we are requiring real-time visuomotor control for our first action it becomes resistant to the influence of the second object's orientation even though grasping a cylinder can afford to be grasped with a wide range of grip orientations.

However, we also did not find our typical size effect under the open-loop condition either. So, it remains possible that the open-loop condition could have possibly caused both actions to be treated as two separate actions (based on their different modes of planning) as opposed to one action sequence, and that is why no orientation or size effect was found. Essentially, the goal of making the open-loop condition enhance the interference effect might have done the exact opposite. Nevertheless, based on the holistic planning hypothesis we should have still found an orientation effect regardless of performing the action under closed- or open-loop conditions. Once again, our results are at odds with the main explanation proposed by previous literature (Haggard, 1998; Hesse & Deubel, 2010; Seegelke et al., 2012, 2013). Instead of trying to modify the paradigm, yet again, to further clarify the nature of our current and previous findings, we believe the next logical step is to backtrack and replicate Hesse and Deubel's (2010) experiment. We hope we can first re-confirm that this paradigm can indeed produce an orientation effect when no size manipulation is applied, before moving forward with more novel experiments to further discover the exact mechanisms of how the brain plans sequential actions.

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CHAPTER 5: REPLICATION OF HESSE AND DEUBEL’S (2010) STUDY

5.1 Introduction

As seen in the last three chapters (chapter 2-4), our approach to investigating how the brain plans sequential grasping actions was heavily influenced by Hesse and Deubel’s (2010) study. Prior to their study, it was demonstrated that the kinematics of performing a grasping action can be influenced by the future task demands (Ansuini et., 2008; Armbrüster & Spijkers, 2006; Cohen & Rosenbaum, 2004; Gentilucci et al., 1997; Haggard, 1998; Johnson-Frey et al., 2004; Marteniuk et al., 1987; Rosenbaum et al., 1992, 1996). However, these results were demonstrated when performing a grasping action on a single object and measuring the effects of action intentions and/or subsequent action with the very same object. Hesse and Deubel (2010) were the first to create a paradigm that would demonstrate that grasping kinematics can also be influenced by future task/action demands associated with another object that is not the immediate target of the first grasping action.

The paradigm they created was intriguing since it was ecologically valid with how we typically plan our daily grasping actions – performing sequential grasping actions with multiple objects. Moreover, their results led to some interesting possible conclusions about how the brain programs sequential grasping actions. It is for this reason we wanted to use the same paradigm but with slight modifications to gain a deeper understanding about how features of a second object in a sequence can directly influence/interfere with the kinematics of grasping the first object. Specifically, Hesse and Deubel (2010) showed that the grip orientation used to grasp the first object (a cylindrical wooden object) was directly influenced by the orientation of the second object (a rectangular wooden object). For example, when the second object was oriented towards the right, participants executed a more rightward grip orientation when grasping the first object.

The main explanation for this result was that the brain utilizes a holistic planning process when planning sequential actions in which elements of the second sequence are blended into the first sequence to strategically benefit the transition towards the overall movement end-goal (e.g., grip orientation already pre-adjusted to pick up the second object). Essentially, each grasping action is not planned in isolation, but the grasping requirements needed for the second action is planned well in advance and can get incorporated, when beneficial, into the first movement plan.

However, in a second experiment, Hesse and Deubel (2010) showed that the orientation of the second object did not influence the first grasping action when participants needed to complete a more difficult task with the first object: placing it on top of a pin instead of simply placing it within a target area. Thus, when the first movement needs more precision (higher difficulty index), the action elements of the sequence are processed independently and there is no functional linkage between both grasping actions (e.g., no grip orientation effect). The holistic planning process is therefore highly dependent on accuracy demands of the first action. Specifically, when the first action can afford it (low level of difficulty) the central nervous system will engage in holistic processing (e.g., planning in advance and strategically integrating elements of the second action into the first action) but when the first action requires more precision, the holistic planning process is not engaged, and each element of the sequence are instead treated as separate/isolated actions.

The results that Hesse and Deubel (2010) produced and their emphasis on the holistic planning hypothesis as their main explanation, nicely converges with the movement integration hypothesis used to explain the one-target advantage when performing sequential reaching actions (Adam et al., 2000, 2001; Bested et al., 2018; Helsen et al., 2001; Khan et al., 2006, 2008, 2010, Mottram et al., 2014, Rand et al., 1997, 2000) and the end-state comfort effects seen in grasping movements (Rosenbaum et al., 1990, 1992, 1993, 1996). However, their results could also be explained via an attentional interference effect. Specifically, it has been shown that properties of objects that are merely distractors can influence the movement kinematics towards a target object (Bonfiglioli & Castiello, 1998; Castiello, 1996; Doyle & Walker, 2011; Howard & Tipper, 1997; Neyedli & Welsh, 2012; Sheliga et al., 1994, 1995; Tipper et la., 2002; Welsh & Elliott, 2004), attention can be simultaneously deployed to all relevant action targets of a sequence (Baldaulf, Wolf, & Deubel, 2006; Baldauf, Cui, & Andersen, 2008), deploying attention to an object will automatically activate its associated action (Chao & Martin, 2000; Grèzes et al., 2003, Murata et al., 1997, Rice et al., 2006, Tucker & Ellis, 1998; Valyear et al., 2006), and motor plans for different targets can be processed in parallel (Chapman et al. 2010; Cisek and Kalaska 2005, 2010; Gallivan et al., 2015, 2016; Klaes et al. 2011; Stewart et al., 2013, 2014, Tipper et al., 1998, Wood et al., 2011). Therefore, the results by Hesse and Deubel (2010, experiment 1) could be driven by the fact that participants deployed attention towards the second object prior to initiating the first movement, and this automatically activated its associated motor prototype (e.g., specific grip orientation) causing interference with the programming of the first action. Whereas, in their second experiment we can assume participants deployed less attentional resource towards the later sequence/second object in order successfully perform the first, more difficult, action accurately, and as result there was no grip orientation effect.

Hesse and Deubel did indeed acknowledge the possibility that their results could also be explained via interference effects driven by automatic motor priming effects. They also admit that their paradigm/data cannot dissociate whether one explanation is more accurate than the other (holistic planning vs. interference effects). This is where we saw an opportunity to further explore and clarify what is exactly happening when features of the second movement in a sequence associated with another object gets integrated into the grasping kinematics towards the first object. To do so, we adopted Hesse and Deubel's (2010) paradigm and applied two crucial modifications.

We used two different sizes of cylinders which were randomized on a trial-by-trial basis for the first object, and we added three possible sizes for the second object (larger, smaller, or same size as the cylinder's diameter) in addition to its three possible orientations. The reason for adding the size factor for the first object was to ensure participants were indeed engaging real-time visuomotor mechanisms (Davare et al., 2007; Desmurget et al., 1999; Goodale et al., 1986; Pisella et al., 2000; Prablanc & Martin, 1992; Rice et al., 2006; Tunik et al., 2005; Westwood & Goodale, 2003). Using the same cylinder as the first object for each trial could have potentially facilitated participants to solely focus on the second object, since they knew what to expect for the first object (features never changed). In addition, because of this, the first action could have been guided by memory mechanisms of the ventral stream (Westwood & Goodale, 2003; Singhal et al., 2013). To avoid this issue, we modified their paradigm so that the first cylindrical object was randomized between two different sizes on a trial-by-trial basis.

Another important modification we applied to Hesse and Deubel's (2010) paradigm was also randomizing the size of the second object in addition to its orientation on a trial-by-trial basis. So, not only could the second object be oriented in three different ways (straight, tilted right, or tilted left) but it could also be one of three sizes (same size as the cylinder's diameter, larger, or smaller). This was a simple way to further test the validity of the holistic planning hypothesis. Specifically, if the holistic planning hypothesis is true the first action should only be influenced by the orientation of the second object and not its size. After all, grasping a cylinder can afford to be grasped by any type of grip orientation, so incorporating the orientation of the second action into the first action could better serve the final action without impairing the first action. However, incorporating the size of the second object (e.g., PGA representation) into the first movement serves no strategic advantage to the overall end-goal since the actor's hand aperture must always close to the "true" size of the first object before grasping the second one. In contrast, if the attentional interference hypothesis is true, all action relevant features (e.g., size and orientation) could interfere with the kinematics of the first action since the interference is driven via an accidental effect, (i.e., visual selective mechanisms implicitly activating the future motor plan in parallel with the current motor plan), not a strategic effect.

We applied this paradigm under three different experimental protocols that varied the task requirements for the second object: participants were required to grasp the second object (chapter 2), participants did not grasp the second object but performed a perceptual judgment about it (chapter 3), and participants grasp the second object, but vision was occluded (Chapter 4). Across all these different experimental protocols, we never observed significant orientation effects as seen in Hesse and Deubel's study. Although an intriguing size interference effect was found (e.g., when size of second object is smaller, participants will reach out to the first object with a smaller PGA relative to when the second object is larger or the same size - albeit this does not happen when the second object is larger or when the second object is to be grasped without vision), it seems that when requiring real-time visuomotor control for the first action, the motor programming becomes less vulnerable to including or being interfered with the features of the second object even in the case where the cylinder can afford to be grasped with a wide range of grip orientations.

Based on the evidence presented in the last three chapters, we believe that Hesse and Deubel's results were most likely driven by the fact that the first object was always the same size, and that the holistic planning hypothesis is most likely not the best explanation for their results. Nevertheless, to refine the theories behind the mechanisms driving the size interference effect seen in our previous studies, it is first necessary to see if we can replicate Hesse and Deubel’s experiment 1 results. If we can replicate their finding, we can safely assume that the reason we never found any orientation effects with our modified paradigm was most likely because a grasping action guided under full real-time visuomotor control is not affected by how the object for the next action is oriented. If that is the case, this will serve an important warning for future studies interested in looking at how the grasping kinematics of an action can be interfered by the features of other objects. However, if we fail to replicate their findings that will reveal that we were previously misled to assume we should be finding an orientation effect. Furthermore, it will also mean that our previous results might be showing an action competition effect – since there is no orientation feature associated with the first object, the orientation of the second object can be successfully inhibited and saved for the later action. However, there is a size feature for both objects, so the size interference effect could be driven by the competition between the two different sizes required for both action plans that are activated in parallel, and due to the nature of how grip aperture tunning works this is only revealed when the second object is smaller (e.g., tuning the aperture towards the larger first object will require the movement of the fingers to pass through the PGA required for the smaller second object, but this not the case if the second object is larger).

Therefore, the goal of this current study is to simply perform a direct replication of the first experiment performed in Hesse and Deubel’s (2010) study. It is also important to note that we directly contacted the main author of the study, Dr. Constanze Hesse, who was kind enough to provide us with some supplementary materials associated to their study (this included more detailed explanations about their methodology in addition to a video of one of the participants performing a trial). This was greatly appreciated since it guided us to try to directly mimic as close as possible their paradigm and experimental setup.

5.2 Methods

5.2.1 Participants

Twenty undergraduate students at Dalhousie University participated in the current study in exchange for partial course credit. All were right-handed, had normal to corrected-to-normal vision, and no history of neurological deficit as ascertained by self-report. Each participant provided informed written consent prior to participation in accordance with guidelines established by the Dalhousie University Research Ethics Board.

5.2.2 Materials

For each trial of the experiment, two wooden objects were presented simultaneously on a white surface table. The stimulus for the first action was a red cylinder located 20cm to the left of the starting switch. The cylinder measured 5.5 cm in height and 4 cm in diameter and the same cylinder was used for all trials. Twenty centimeters above the location of the cylinder was a marked circled area colored in either red or yellow. The red circle was 4.5 cm in diameter and the yellow circle was 6 cm. This indicated the target location of where the participants needed to move the cylinder. The stimulus for the second action was a black rectangle bar measuring 5 cm in length and 2cm in depth and located 20 cm to the right of the target circle. The same bar was used throughout the experiment. However, on a trial-by-trial basis the bar could be oriented straight (0°), 45 ° to the right, or 45 ° to the left.

An Optotrak 3020 (Northern Digital, Waterloo, ON, CANADA) system was used to record at 200 Hz the three-dimensional locations of IREDs placed on the distal phalanx of the thumb, the lateral surface of the distal phalanx of the index finger, and the styloid process of the radius of the right upper limb. Participants wore liquid–crystal occlusion glasses (PLATO

Translucent Technologies, Toronto, ON, Canada) to block visual input during the experiment as indicated in the procedure. A tone was presented as the signal for participants to initiate the first action (800 Hz; 250 ms). A chin rest was also used and placed at the edge of the table in front of the first object to maintain a constant head position throughout the experiment – it is important to note that in our previous experiments (chapter 2-4), we never used a chin rest.

5.2.3 Procedure

Participants were seated comfortably in front of a table during all experimental trials with their head placed upon a chin rest in a well-lit room. Each participant performed six practice trials to ensure they understood the requirements of the task. They were first instructed to depress a release button using their pinched right index finger and thumb at the start of each trial. The LCD glasses were opaque at the start of each trial while the experimenter positioned the target objects. Once the objects were correctly positioned the experimenter triggered the start of the trial and the glasses turned transparent to reveal the environment. The start tone was presented 1000ms after the preview period.

At the sound of the start tone, participants were required to reach, grasp, and pick up (with right thumb and right index finger) the cylinder and to place it in the marked target circle area. The target circle was either the red circle (difficult condition) or the yellow circle (easy condition). However, the target circle was presented in blocks of trials, and it was counterbalanced among participants in terms of whether they performed the first block of trials under the ‘difficult condition’ or the ‘easy condition’ first. Once the first object was placed within the circle area, participants were then required to reach, grasp, and pick up the rectangular bar along the front-to-back axis and place it in the center of the workspace (no specified location).

Participants were instructed to complete each action as quickly and accurately as possible. The LCD glasses returned to an opaque state 4000ms after the initiation tone, such that vision was available during the entire task but occluded at the end of each trial before the stimuli for the next trials were arranged. Each participant performed a total of 60 trials (10 trials for each type of orientation performed under the two different blocks).

5.2.4 Data Processing

Offline, a custom Python routine was used to extract movement kinematics from the raw 3D data collected during the experiment. The data was filtered using a second-order dual pass Butterworth filter employing a low-pass cut-off frequency of 12Hz. Measures extracted from the primary action (the movement to the first object) included reaction time (RT; the time from the onset of the auditory go signal until the velocity of the IRED on the wrist exceeded 30 mm/s for 5 consecutive time samples), movement time (MT; the time from when the wrist IRED exceeded 30 mm/s for 5 consecutive time samples until it dropped below 30 mm/s for 5 consecutive time samples), and grip orientation (the angle of the horizontal projection of the index finger and thumb – 0 ° in orientation corresponded to a perfect sagittal line projection, clockwise projections from that line is defined as positive angles and anticlockwise projections as negative angles). Interactive routines enabled the experimenter to ensure the automated algorithms chose the appropriate values in cases of missing IRED positions. All dependent measures were analyzed within participants, and trials were rejected if any of the measures fell beyond ±3 standard deviations of the individual participants' mean for that measure (less than 1% of trials were rejected from data analyses).

Each dependent measure was analyzed using a 3 (orientation of bar) x 2 (placing difficulty) repeated-measures ANOVA ($\alpha = 0.05$). Sphericity was evaluated using Mauchly's test ($\alpha = 0.05$), and Greenhouse–Geisser corrections were applied if needed.

5.3 Results

5.3.1 Grip Orientation

No significant interaction was found between the orientation of the bar (second object) and the placing difficulty, F (2,38) = 1.07, p= 0.35, $\eta_p^2 = 0.05$. There was no main effect of placing difficulty, F (1, 19) = 0.08, p = 0.78, $\eta_p^2 = 0.005$, and no main effect of orientation of the second object, F (2, 38) = 1.19, p = 0.32, $\eta_p^2 = 0.06$, as seen in Figure 8.

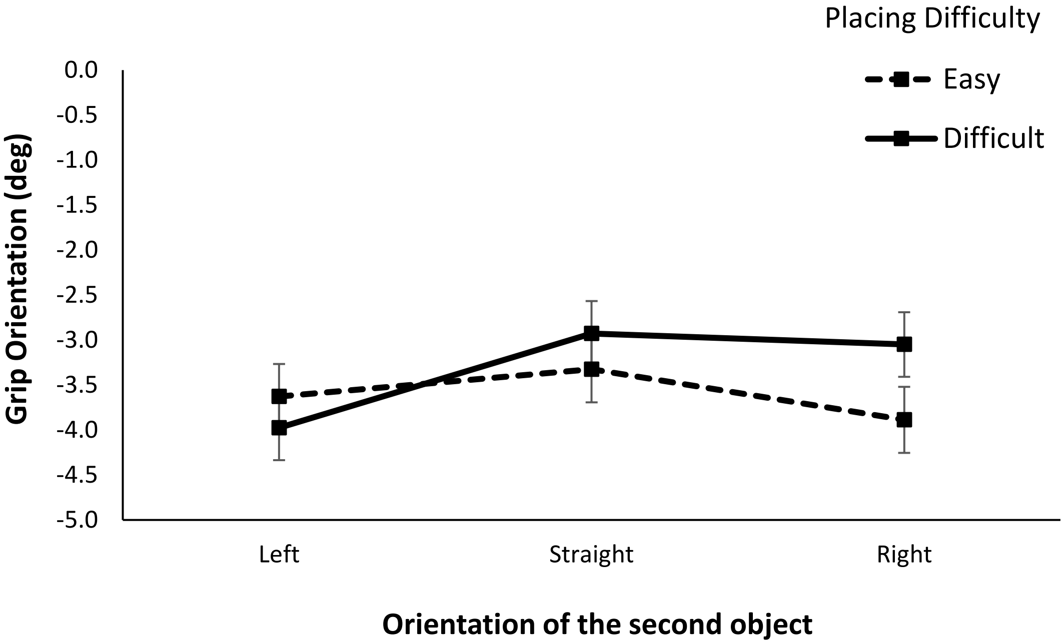

Figure 8. Mean grip orientation when performing a grasping action to the first object in relation to the orientation of the second object. The easy task (bigger placing area) is depicted with the dashed lines and difficult task (smaller placing area) is depicted in with the solid black line. Error bars indicate SEM. No significant differences were found.

5.3.2 Reaction time

There was no significant interaction between the orientation of the second object and the placing difficulty, F (2, 38) = 0.36, p = 0.69, $\eta_p^2 = 0.02$. There was no main effect of orientation of the second object, F (2, 38) = 0.49, p = 0.62, $\eta_p^2 = 0.03$, and no main effect of placing difficulty, F (1, 19) = 1.83, p = 0.19, $\eta_p^2 = 0.09$.

5.3.3 Movement time

There was no significant interaction between the orientation of the second object and the placing difficulty, F (2, 38) = 0.12, p = 0.89, $\eta_p^2 = 0.01$. There was no main effect of orientation of the second object, F (2, 38) = 0.11, p = 0.82, $\eta_p^2 = 0.01$, and no main effect of placing difficulty, F (1, 19) = 1.3, p = 0.26, $\eta_p^2 = 0.07$.

5.4 Discussion

The goal of this study was to perform a replication of Hesse and Deubel's (2010) study to clarify our own previous findings (Chapter 2-4). Despite making the effort of copying their exact methodology, we failed to confirm any of the results they reported. As seen in all our previous studies, we once again found no evidence that the orientation of the second object affected how the participants oriented their grip orientation to grasp the first object. We also surprisingly did not find any significant effect based on the difficulty of the placing task for both MTs and RTs.

However, it is important to note that the difference in the index of difficulty (Fitts, 1954) between the two placing task is merely 0.3 bits. Thus, when taking that into consideration, it is not surprising that there is no significant difference in MT – which also suggest that Hesse and Deubel's results were atypical (e.g., typical studies will report a difference in MT when the IDs being compared have a difference of at least greater than 1 – see Rand et al. (1997, 2000) for examples). As for the RTs, it seems the participants in Hesse and Deubel's study were initiating the first action faster than the participants in this current study from about 100ms, as seen in Table 1. This could potentially explain why there is a difference between our results. But that explanation would go against the holistic planning hypothesis. After all, the more time spent preplanning the action the more likely the central nervous system could incorporate the second action into the first action. Therefore, if our differences in RTs is the main explanation as to why we are finding different results it would be due to an explanation that favours the attentional interference hypothesis: Participants have less time to inhibit the motor prototype (e.g., grip orientation) automatically elicited by deploying attention towards the second object prior to executing the first action. As a result, the motor prototype leaks into the programming of the first action. Whereas, in our study, the 100ms extra could be the necessary threshold to successfully inhibit the action prototype of the second object, so the grip orientation associated with the second object doesn't leak into the initial motor program.

Table 1

Comparing the average RT for the easy and difficult placing task from Hesse and Deubel's study and our current study.

	Hesse and Deubel (2010)	Current Study
Average RT for easy task	242ms (SE:13)	346 ms (SE:17)
Average RT for difficult task	260ms (SE:12)	357 ms (SE:20)

Nevertheless, this is merely a speculation in effort to try to find a possible reason as to why we did not come close to replicating their results. Based on our communication with the main author, both studies instructed participants to start and perform the movements as quickly as possible while maintaining their accuracy. Most importantly, both studies had no time limit to when participants could initiate the action. But when looking at RTs from our 20 participants, only two were within the faster RT range that Hesse and Deubel (2010) reported. So, it remains a bit of a mystery why their participants were on average faster than the ones in the current study. One difference that could potentially explain this is that within their sample they included graduate students, whereas our sample were mostly first year undergraduates. Thus, it could be argued that our participants were more naïve to experimental testing procedures whereas they might have recruited a sample that were more experienced in reacting to tones and getting into the flow of an experiment.

Another difference between our studies was the type of motion capture system used. They had an electromagnetic motion tracking device in which the cords attached to the sensors on the hand were visibly thicker than the cords/sensors of our optical motion capture system. Thus, another speculation as to why we got different results, could be because in our study participants felt "less attached" to a machine and the grasping actions felt more natural. Whereas, in their study the potential awkwardness of the cords might have made the grasping action feel less natural and this somehow made them more vulnerable to incorporating the grip orientation of the second action. It has been demonstrated that grasping that is consciously monitored (as opposed to the natural unconsciously monitored grasping process) is more vulnerable to perceptual intrusions (Navon & Ganel, 2020), suggesting that the dorsal and ventral streams are more likely to interact when forced to perform a grasp that is not considered natural. Therefore, it is possible that due to the fitting of the cords and sensors, participants in Hesse and Deubel's study where more likely to recruit more ventral stream processing during the first grasping action which made the action more vulnerable to interferences.

Also, their participants were given monetary reward for participation, but our participants received partial course credit (e.g., bonus points). It is difficult to conceptualize how this could have affected the results, although one could argue that receiving money is considered more ‘rewarding’ and perhaps this made participants more interested/engaged in the overall experiment which affected the type of processing deployed to complete the trials – it is well documented that stimuli associated with higher rewards will capture attention more effectively (Anderson, 2016; Chelazzi et al., 2013; Failing & Theeuwes, 2018) and influence movement trajectories (Chapman et al., 2015, Moher et al., 2015) to a greater extent than stimuli associated with lower rewards. But it is important to note, that this is reported with different stimuli within the same experiment not across different experiments (e.g., comparing the effects of a distractor associated with high-reward versus one associated with low-reward).

Regardless of what caused the differences in our results relative to Hesse and Deubel’s (2010) results, we can at least now determine that, under our setting with our equipment and our instructions, the first grasping action is not influenced by the orientation feature of the second object even if the first object remains the same throughout the experiment, and even when there is no changing size feature for the second object. Thus, we can now breakdown our previous results more precisely and further explore what was causing the size interreference effect seen across our studies.

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CHAPTER 6: GENERAL DISCUSSION

6.1 Summary of results

Our main goal was to further refine our current understanding about how sequential grasping actions are programmed and executed. We wanted to explore whether the kinematics (e.g., PGA and grip orientation) of the first grasping action of a sequence would be affected by the features of the second object/action of the sequence – more specifically what specific characteristics of the second object (e.g., orientation vs. size) can influence how the first grasping action is executed and why it happens (e.g., action efficiency, motor interference, or perceptual interference).

In our first study (chapter 2), we showed that when participants grasped the first object (e.g., cylinder) their grasping kinematics were not influenced by how the second object (e.g., rectangular bar) was oriented. However, it was shown that when the second object was smaller than the diameter of the cylinder, participants PGA was significantly smaller when grasping the cylinder relative to when the second object was larger or the same size. This pattern of result was a bit surprising since we used a paradigm based on Hesse and Deubel's (2010) study in which they showed that the orientation of the bar had a very strong effect on the grip orientation used to grasp the cylinder – which led them to favour the holistic planning hypothesis (e.g., features of the second action implemented into the first action for strategic benefit). Although we added size features to both the first (e.g., to study grasping as an online visuomotor control process) and second object (e.g., to see if a feature that serves no benefit to be prepared in advance would still interfere with the first action) in our experiment, we were still expecting to replicate their orientation effect.

Specifically, we predicted that an orientation effect in addition to a size effect would favor the attentional interference hypothesis (e.g., features of second object interfere with the programming of the first action due to attentional mechanisms and implicit motor processing - regardless of whether its advantageous or not) which was an alternative explanation from the holistic planning hypothesis. Therefore, since the only feature that seemed to influence the kinematics of the first action was the smaller object, it led us to possibly believe that when participants are required to fully engage in online visuomotor processing for the first object/action (by varying size on trial-by-trial basis) the first action is no longer influenced by the orientation of the second object. However, since it was also not influenced by the size of a larger object, it led us to question whether the unique interference effect found in this experiment could be because preparing a future action towards a smaller object will require more online control than the initial action towards a larger object (Grol et al. 2007). Therefore, perhaps more attentional resource is dedicated towards the second action when it's a smaller object, and this causes its associated size prototype to interfere with the tuning of the aperture of the first grasping action.

To clarify our results, a second study was conducted (chapter 3) where instead of grasping the second object participants would now be required to perform a perceptual judgment about it (e.g., describing the orientation and size relative to the first object). If our previous results were driven by the specific action requirement of the second object, the smaller second object should no longer interfere with the first grasp if a perceptual task is performed instead (no action required but object still needs to be processed). Once again, despite not performing any actions to the second object, the same pattern of result was found: no orientation effect but a size effect, albeit only when the second object is smaller. These pattern of results, although it left us a bit puzzled for the exact neural mechanisms at play, strongly suggested that the interference effects described in previous studies (Haggard, 1998, Hesse and Deubel, 2010; Seegelke et al., 2012, 2013) could have been driven by attentional mechanisms and not due to holistic planning processes. After all, the fact we found any interference effect with this experiment (e.g., only one action to be performed) strongly violates the core tenets of the holistic planning hypothesis.

However, we still could not rule out the fact that it is possible that that participants are not actively processing the orientation of the second object in advance of the first action, since they are now preoccupied with size processing because of our size manipulations, and that is why we failed to find any orientation effects for our first and second experiment. Thus, we performed our third study (chapter 4) where the same paradigm as our first experiment was used for a block of trials (closed-loop condition) and for the other block of trials we added the crucial modification of occluding vision for the second action (open-loop condition). So, participants indeed had full-vision when performing the first action but after they would lose vision (via LCD glasses turning opaque) and the second action would be performed under memory-guided mechanisms. This naturally forced the participants to fully process all the relevant features (e.g., size and orientation) of the second object prior to performing the first action. For the closed-loop condition, we again found a similar pattern of result as our two other previous studies: the first grasping action is only affected by the smaller second object but not the larger second object, and not affected by the second object's orientation. Surprisingly, for the open-loop condition, there was still no significant orientation effect, and no size effect.

We were now starting to be convinced that the orientation of the second object had no influence on the grip orientation used to grasp the first cylinder when performed under full visuomotor control – thus, explaining the difference between our results and the results from Hesse and Deubel's study (2010). However, the fact we also did not find our typical size effect for the open-loop condition suggested that participants were most likely applying a different mode of processing for this task now. Specifically, since we were now forcing the participants to program a memory-guided action for the second object, and this will of course heavily rely on ventral stream processing (Cohen, et al., 2009; Gentilluci et al., 1996, Hu & Goodale, 2000; Rossetti, 1998, Singhal et al. 2013; Westwood et al., 2000, 2001; Westwood & Goodale, 2003) in which the features of the second object will be held in memory as a perceptual trace that will later guide the following action. Therefore, the act of actively storing the features in memory outside of the grasping circuit could simultaneously make the first action more immune to its interferences – unlike planning another action fully guided by real-time visuomotor control which potentially causes a competition between action plans in which overlapping features can interfere.

Nevertheless, based on the holistic planning hypothesis we should have still found an orientation effect regardless of performing the action under closed- or open-loop condition. If anything, it could be easily argued that the open-loop condition should have exaggerated the effect since it is even more advantageous to implement the orientation of the second object into the first grasping action within this specific sequential scenario (e.g., reducing the memory load for the second motor plan). So, once again, our results were at odds with the main explanation proposed by previous literature exploring sequential effects in grasping (Haggard, 1998; Hesse & Deubel, 2010; Seegelke et al., 2012, 2013). However, instead of trying to modify our experimental paradigm, yet again, to further clarify the nature of our current and previous findings, it was deemed essential that we performed a replication of Hesse and Deubel's study (2010) to re-confirm that this paradigm can indeed produce an orientation effect when no size manipulation is applied.

Despite making the effort of copying their exact methodology, we failed to obtain any of the results they reported. As in all our previous studies, we once again found no evidence that the orientation of the second object affected how the participants oriented their grip orientation to grasp the first object. However, based on our RT results, there might have been a difference in the mode of processing utilized between the different set of participants. Specifically, our participants were on average consistently slower to initiate the first action than their set of participants (see Table 1). Although we made our best attempt to deliver the experiment in the same way as Hesse and Deubel (2010), in section 5.4 we list factors that were not the same across both experiments which could have possibly played a role in the drastic difference in results. We also cannot ignore the fact that there was never a direct follow up study, or a similar study reported in the literature (e.g., exploring sequential effects when grasping two objects consecutively with a precision grip) – although Seegelke et al. (2012, 2013, 2015) performed similar studies, which explored similar concepts and promoted similar conclusions as Hesse and Deubel, their task consisted of grasping one cylinder with a power grasp and sliding it sequentially across various differently orientated target areas. Therefore, since this is not a well-established paradigm that has never been replicated, it is quite possible that Hesse and Deubel captured an anomaly and the results reported are not replicable.

Even though we were perhaps misled in thinking this was a good paradigm to further explore the mechanisms of how the central nervous system programs and coordinates sequential grasping actions, we nevertheless still found a unique size interference effect across our experiments. Now that we have confirmed - under our setting, our instructions, and our equipment – that the programming of the first action does not get interfered by the orientation feature of the second object, we can now take a deeper theoretical dive into why the second object only interferes with PGA of the first action when it is a smaller object relative to the first object.

6.2 Parallel processing and competition for action: the aperture tuning effect

Within our modified version of Hesse and Deubel's (2010) paradigm, each object varied in size on a trial-by-trial basis, whereas the orientation feature was only a feature associated with the second object. Therefore, it is worth speculating that the size interference effect we found might have emerged due to the competition between the two different sizes required for both action plans that were activated in parallel. More specifically, it is likely that participants were deploying attention towards the second object prior to initiating the first action (Baldaulf, Wolf, & Deubel, 2006; Baldauf, Cui, & Andersen, 2008), and that causes the implicit activation of its associated motor prototype (Chao & Martin, 2000; Grèzes et al., 2003, Murata et al., 1997, Rice et al., 2006, Rizzolatti & Luppino, 2001; Tucker & Ellis, 1998; Valyear et al., 2006), which would directly compete and interfere with the motor programming of the first action (Cisek and Kalaska 2005, 2010; Chapman et al. 2010, Gallivan et al., 2015, 2016; Klaes et al. 2011; Neyedli & Welsh, 2012; Stewart et al., 2013, 2014, Tipper et al., 1998, Wood et al., 2011) and this happens regardless of whether the process is driven by attention-for-action or attention-for-perception (Hommel, 2009; Kikumoto & Mayr, 2020; Takacs et al., 2020).

Although most of the citations presented in the above explanation are from results captured by reaching experiments, it is important to highlight that there is indeed evidence via neuron recordings in monkeys that the AIP can have multiple grasping prototypes activated in parallel prior to executing an action (Bauman et al., 2009 – see Gallivan & Wood (2009) for further explanations). It has also been shown that selective PMv neurons that represent a specific grasp prototype will discharge by simply seeing (no action performed) an object that affords that type of grasp (Rizzolatti & Luppino, 2001). Thus, based on past evidence, it is possible that the size interference effect we found across our experiments could indeed be driven by the parallel activation of the different grasping prototype required for each object (e.g., one requiring big PGA vs. small PGA). Specifically, during our experiments, PGA became smaller when the first object is in competition with a smaller second object. However, if this explanation is true, it would then be assumed that when the second object is larger the same interference effect would be seen, but in this case, participants would reach with a larger PGA for the first grasping action. However, across all the experiments presented within this dissertation, we never once found a size effect driven by the larger second object only always the smaller object. Why?

One explanation that could clarify this confusion is that the competing motor prototype (elicited by the second object of the sequence) might directly interfere with the kinematics of the first grasp only if it directly overlaps within the scaling range of that grip aperture. Since participants were starting with their thumb and index finger pinched together, the fingers must move through the PGA required for the smaller second object as they tune their aperture towards the larger first object. Whereas, due to the positioning of the fingers at the start, this scenario does not happen in the context of a larger second object since PGA for the first smaller object will be attained without needing to move through the PGA required for the larger object – since there is no overlap, the second action can presumably be successfully inhibited, and there is no interference. In contrast, when the second action does overlap, the implicit motor priming caused by the second object becomes harder to inhibit and causes an interference effect when shaping the fingers to grasp the first object (e.g., using a significantly smaller PGA for grasping the first object when the second object is smaller relative to when it is the same size or larger than the first object).

To conceptualize this further, it would be as if there are populations of aperture-tuned neurons within AIP and when two grasping prototypes are activated in parallel that rely on similar populations of neurons, the selected PGA deployed to perform the grasping action will be affected by the non-selected prototype. This concept would resemble a similar mechanism to how movement trajectories are selected based on the vector sum of the activation levels of directionally-tuned motor cortical neurons (Georgopoulos, 1995). Nevertheless, based on that assumption, it would then be predicted that if the participants' fingers were stretched apart instead of pinched together at the start location, we would get the opposite effect: the aperture tuning for grasping the first smaller object would then need to move through the larger PGA required for the larger second object ('PGA tuning overlap') thus causing a larger PGA – and in this case the smaller second object would no longer cause any interference.

A simple way to test this would be to perform the same study as experiment 1 (chapter 2) but with the addition of including trials where participants are starting with their fingers stretched out instead of pinched together to see if that would indeed produce a larger PGA when the second object is larger than the first. However, instead of relying on a sequential task, a more effective study could be designed that would allow us to better capture the interference effect potentially caused by the parallel activation of competing grasping actions. This could be done by briefly presenting two objects (side by side), in which one of them would eventually be cued for action, and participants would then be required to grasp that object under a strict time limit (to prevent the less inhibition possible). The objects could either be the same size (control conditions) or one would be larger/smaller than the other, and participants would either start with their fingers pinched together or stretched apart. Unlike in a sequential action situation, in this case participants are faced with target uncertainty till movement onset; thus, it would be expected that if a size interference effect can indeed be caused by the parallel activation of two overlapping grasp plans, then we should capture a more robust interference effect under this experimental setup. Specifically, when the non-target object is bigger, relative to the same size or smaller than the target object, we should see participants grasp with a significantly larger PGA only when they start with fingers stretched apart and not when starting with fingers pinched together. In contrast, when the non-target object is smaller, participants will grasp with a smaller PGA only when they start with their fingers pinched together.

If such an experiment would indeed demonstrate a clear dissociation in the PGA results between the starting position of the fingers and the size of the non-target object, this would confirm that, as seen with movement trajectories (Cisek and Kalaska 2005, 2010; Chapman et al. 2010, Gallivan et al., 2017; Klaes et al. 2011; Neyedli & Welsh, 2012; Stewart et al., 2013, 2014, Tipper et al., 1998, Wood et al., 2011), the programming of a grasping action can also be affected based on what other grasping prototype gets activated in parallel during the movement planning phase. In addition, to further clarify that this is indeed a true motor effect (driven by dorsal stream processing) and not a process initially driven by perception (ventral stream processing), the same experimental procedure could be applied but the non-target object would be presented within a size illusion context (e.g., perceptually appears bigger but it is physically smaller than the target object). In that case, if the PGA is still influenced by the true size of the object (and not the illusory size) this would further clarify that the interference is not only happening within the grasping circuit, but it also originates from there. Moreover, establishing a strong behavioural paradigm that would reveal such results, would allow researchers to explore more precisely the neural correlates that are directly causing this behavioural effect. This would then provide a much better experimental/theoretical foundation to try to see if this ‘aperture tuning' effect is also at play when planning sequential actions – as the results of this dissertation suggest so. This could also lead future research to see if there is the equivalent of an 'orientation tuning' effect, and whether it is possible to detect a size and orientation interference effect within one grasping action (e.g., PGA and grip orientation) – as the experiments in this dissertation (Chapter 2-4) attempted to do.

6.3 Better approaches for future sequential grasping research

The appeal to studying grasping in the context of sequential actions was because it enables us to study a process that better captures what we typically do in a 'real-life' context. As explained in the introduction, most of our understanding about the neuroscience of grasping is currently based on studies where one grasping action is performed towards one single object. It is for this reason we were interested in Hesse and Deubel's (2010) study, since it seemed, at the time, like a good starting point to further develop our understanding about how a grasping action is affected by the next action/object of a sequence. However, now that we have failed to replicate their findings, we also realize that their paradigm is most likely not the best experimental layout to approach the sequential grasping problem.

After all, some of the earliest research looking at how non-targets interfere with the movement of reaching towards a target, would have most likely predicted that the orientation of the second object would not influence the first action within this layout since the second object is not located near the path towards the first action (e.g., action-centered based attentional frame of reference, Meegan & Tipper, 1998; Pratt & Abrams, 1994; Tipper et al., 1992); Therefore, it could be that the orientation of the bar would have much greater influence when grasping the cylinder if it was placed somewhere in between the location of the starting area and the cylinder. Future experiments exploring sequential grasping actions should strongly consider (or actively manipulate) where the objects are situated in reference to the action-centered attentional landscape of the actor, since that could strongly impact whether the object associated with the second action of the sequence will influence the first action.

Furthermore, to truly mimic grasping within a ‘real-life’ context it would be essential to make each action sequence more functionally linked together or at least related to a common goal. Essentially, the holistic panning process might indeed still be a real phenomenon when measured under the right circumstances. In the context of the current paradigm, the cylinder and the bar are never directly related to the same goal or function, and it was also never explicitly quantified that incorporating the orientation of the bar into the grip orientation used to grasp the cylinder provides any true biomechanical benefit to the overall movement – we essentially just took Hesse and Deubel’s results for granted. Therefore, for future experiments it would be essential to build an experimental layout where there is a quantified benefit associated with incorporating a specific feature associated with the object of the second segment into the grasping plan for the object of the first segment. This could then be compared with another condition where there is no such benefit for incorporating that feature and see how the kinematics of the first grasping action is affected accordingly. In addition, making the sequence more meaningful by incorporating rewards and penalty constraints could indeed provide much more meaningful results than simply picking up two objects associated with no value/consequence.

Essentially, when we perform our daily activities, our motor system has learned to solve the redundancy problem (i.e., for every goal driven action there are several different possibilities on how to successfully execute the appropriate motor behaviour to attain the desired outcome) by choosing the most optimal way to execute the action to maximize the positive outcomes (e.g., successfully picking up the wine glass) and minimize the negative outcomes (e.g., knocking over the wine glass on my laptop). Therefore, incorporating rewards and penalties associated with the movement outcomes of each object within a sequential task and functionally linking them together could indeed make the task more meaningful/ecological and give us a deeper understanding about how we control sequential grasping movements within our typical daily environments. Creating an experimental paradigm in which incorporating a feature of the second object into the kinematics of the first grasping action would be the most optimal way to perform the sequence (e.g., it increases the chances of obtaining a reward and decreases the chances of obtaining a penalty), but this is not explicitly obvious to the participants, would indeed be a very interesting approach to studying sequential grasping behaviour. This would also allow us to see when (or if) the motor system will adapt its grasping kinematics to perform the most optimal grasp possible. Specifically, when it comes to aiming to an optimal movement endpoint, it has been shown that participants will only start to aim at the optimal location once they have received enough experience with the task and received consistent feedback about their performance (Neyedli & LeBlanc, 2017; Neyedli & Welsh, 2013, 2014). Thus, it is possible that the grasping hand would also need sufficient experience/feedback before adopting the most optimal grasp for the initial action of a sequential task.

Another a crucial piece of advice for future research is to ensure that if you create a modified paradigm based on previous research, make sure you can indeed replicate their findings before moving forward. Not only have we failed to replicate Hesse and Deubel's (2010) study as seen in chapter 5 and mentioned throughout this current chapter, but we also failed to replicate Castiello's (1996) influential study. Specifically, we did not find any evidence that a distractor fruit interferes with how you grasp (e.g., PGA) another target fruit, even when performed under a monocular condition (Coughlin, LeBlanc, & Westwood, 2016). So, in the case of this dissertation, we were misled by two studies into believing assumptions regarding the design of our experimental paradigm that were indeed not accurate assumptions. It is for that reason we advise future research to take the time to validate and replicate pas results – that have not been extensively researched (e.g., no follow up or other similar studies)- prior to creating/modifying new experimental paradigms based on those results. After all, there seems to be many false positives results published, even among some of the most prestigious journals (Camerer et al., 2018).

6.4 Conclusion

The overall goal of this thesis was to investigate whether characteristics of a second object within a sequential task can directly influence how you grasp the first object of the sequence. More specifically, it was explored whether the size and/or orientation features of the second object would interfere with the grasping kinematics (e.g., PGA and grip orientation) towards the first object. The type of task requirement associated with the second object was also varied across three different experiments: participants were required to grasp the second object (chapter 2), participants did not grasp the second object but performed a perceptual judgment about it (chapter 3), and participants grasp the second object, but vision was occluded (Chapter 4). Across all these different experiments, not once did the results reveal that the orientation of the second object influenced the grip orientation selected to grasp the first object. However, when participants are required to grasp the second object (with vision) or perform a perceptual judgment about it, participants reached out with a smaller PGA to grasp the first object when the second object was smaller relative to when it was the same size or larger than the first object.

Since these results were not consistent with previous results reported by Hesse and Deubel (2010), we conducted a replication of their study and failed to produce the same results (e.g., no orientation effect). The data presented within this dissertation suggest that the second object within a sequential task will only interfere with the grasping kinematics of the first object when both action plans have overlapping features, and this is not dependent on providing a strategic benefit to the overall movement. These results are speculated to have emerged due to a motor interference effect driven by the parallel encoding of grasping actions within the anterior intraparietal area (i.e., the grasping circuit).

6.5 References

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APPENDIX A: CHAPTER 2 (EXPERIMENT 1) DESCRIPTIVE STATISTICS

Table 2. *Mean PGA (mm) when performing a grasping action to each type of cylinder (first object) in relation to the size (relative to the first cylinder's diameter) and orientation of the second object.*

	First Object:	
Second Object (size/orientation):	Cylinder (6cm)	Cylinder (5cm)
Larger/Left	87.42 (8.5)	80.89 (8.2)
Larger/Straight	86.69 (7.9)	81.03 (8.6)
Larger/Right	87.12 (7.4)	81.39 (8.5)
Same/Left	86.86 (7.9)	81.83 (8.2)
Same/Straight	87.67 (7.3)	80.45 (8.0)
Same/Right	87.12 (8.2)	81.31 (7.6)
Smaller/Left	86.36 (8.2)	80.58 (8.3)
Smaller/Straight	86.86 (7.8)	80.88 (8.4)
Smaller/Right	86.16 (8.4)	81.16 (7.9)

Table 3. *Mean grip orientation (degrees) when performing a grasping action to each type of cylinder (first object) in relation to the size (relative to the first cylinder's diameter) and orientation of the second object.*

	First Object:	
Second Object (size/orientation):	Cylinder (6cm)	Cylinder (5cm)
Larger/Left	-2.36 (13.4)	-5.47 (13.5)
Larger/Straight	-3.94 (12.3)	-3.66 (13.8)
Larger/Right	-2.39 (12.9)	-3.22 (13.2)
Same/Left	-3.70 (12.9)	-2.94 (14.2)
Same/Straight	-2.31 (13.2)	-4.14 (13.1)
Same/Right	-3.15 (13.4)	-3.56 (13.0)
Smaller/Left	-3.50 (13.4)	-5.12 (13.2)
Smaller/Straight	-2.10 (13.1)	-4.42 (13.8)
Smaller/Right	-3.23 (12.9)	-3.86 (13.9)

Table 4. *RT (ms) when performing a grasping action to each type of cylinder (first object) in relation to the size (relative to the first cylinder's diameter) and orientation of the second object.*

Second Object (size/orientation):	**First Object:** Cylinder (6cm)	Cylinder (5cm)
Larger/Left	476 (204)	483 (201)
Larger/Straight	494 (200)	481 (189)
Larger/Right	478 (182)	461 (184)
Same/Left	475 (193)	470 (175)
Same/Straight	460 (200)	494 (196)
Same/Right	487 (166)	485 (199)
Smaller/Left	480 (192)	477 (183)
Smaller/Straight	480 (198)	488 (161)
Smaller/Right	488 (175)	468 (208)

Table 5. *MT (ms) when performing a grasping action to each type of cylinder (first object) in relation to the size (relative to the first cylinder's diameter) and orientation of the second object.*

Second Object (size/orientation):	**First Object:** Cylinder (6cm)	Cylinder (5cm)
Larger/Left	562 (93)	562 (91)
Larger/Straight	555 (95)	568 (99)
Larger/Right	550 (77)	558 (89)
Same/Left	561 (84)	553 (83)
Same/Straight	555 (88)	563 (82)
Same/Right	573 (96)	557 (82)
Smaller/Left	558 (88)	568 (89)
Smaller/Straight	558 (89)	574 (94)
Smaller/Right	569 (90)	550 (89)

Table 6. *tPGA (ms) when performing a grasping action to each type of cylinder (first object) in relation to the size (relative to the first cylinder's diameter) and orientation of the second object.*

Second Object (size/orientation):	**First Object:** Cylinder (6cm)	Cylinder (5cm)
Larger/Left	440 (82)	436 (88)
Larger/Straight	436 (85)	442 (92)
Larger/Right	435 (74)	436 (87)
Same/Left	444 (81)	436 (78)
Same/Straight	433 (82)	443 (78)
Same/Right	443 (86)	431 (81)
Smaller/Left	440 (86)	439 (88)
Smaller/Straight	436 (81)	449 (86)
Smaller/Right	451 (88)	429 (87)

APPENDIX B: CHAPTER 3 (EXPERIMENT 2) DESCRIPTIVE STATISTICS

Table 7. *Mean PGA (mm) when performing a grasping action to each type of cylinder (first object) in relation to the size (relative to the first cylinder's diameter) and orientation of the second object.*

	First Object:	
Second Object (size/orientation):	Cylinder (6cm)	Cylinder (5cm)
Larger/Left	83.56 (8.9)	79.16 (7.6)
Larger/Straight	84.22 (7.9)	79.33 (8.3)
Larger/Right	84.58 (8.4)	79.40 (8.0)
Same/Left	83.68 (7.9)	79.34 (8.5)
Same/Straight	84.89 (8.7)	79.37 (8.6)
Same/Right	84.11 (8.5)	79.30 (8.7)
Smaller/Left	83.22 (8.6)	78.91 (7.5)
Smaller/Straight	83.34 (8.5)	78.16 (7.9)
Smaller/Right	83.45 (9.2)	78.92 (8.4)

Table 8. *Mean grip orientation (degrees) when performing a grasping action to each type of cylinder (first object) in relation to the size (relative to the first cylinder's diameter) and orientation of the second object.*

	First Object:	
Second Object (size/orientation):	Cylinder (6cm)	Cylinder (5cm)
Larger/Left	-6.99 (17.4)	-7.95 (18.4)
Larger/Straight	-7.80 (17.1)	-6.84 (17.4)
Larger/Right	-6.52 (17.5)	-7.92 (17.8)
Same/Left	-9.21 (17.3)	-7.86 (16.9)
Same/Straight	-6.55 (17.3)	-7.67 (15.8)
Same/Right	-4.28 (17.9)	-6.07 (16.3)
Smaller/Left	-7.87 (17.9)	-6.92 (17.4)
Smaller/Straight	-6.72 (18.6)	-9.73 (15.3)
Smaller/Right	-8.61 (16.6)	-6.72 (17.5)

Table 9. *RT (ms) when performing a grasping action to each type of cylinder (first object) in relation to the size (relative to the first cylinder's diameter) and orientation of the second object.*

	First Object:	
Second Object (size/orientation):	Cylinder (6cm)	Cylinder (5cm)
Larger/Left	655 (299)	655 (328)
Larger/Straight	604 (274)	651 (276)
Larger/Right	644 (355)	665 (371)
Same/Left	638 (341)	681 (422)
Same/Straight	631 (295)	658 (282)
Same/Right	655 (357)	673 (346)
Smaller/Left	610 (288)	655 (462)
Smaller/Straight	676 (482)	614 (274)
Smaller/Right	683 (404)	632 (335)

Table 10. *MT (ms) when performing a grasping action to each type of cylinder (first object) in relation to the size (relative to the first cylinder's diameter) and orientation of the second object.*

	First Object:	
Second Object (size/orientation):	Cylinder (6cm)	Cylinder (5cm)
Larger/Left	669 (130)	671 (122)
Larger/Straight	696 (138)	661 (144)
Larger/Right	675 (145)	664 (136)
Same/Left	651 (125)	671 (137)
Same/Straight	671 (126)	649 (113)
Same/Right	673 (121)	686 (140)
Smaller/Left	673 (142)	671 (125)
Smaller/Straight	666 (125)	662 (123)
Smaller/Right	679 (132)	679 (142)

Table 11. *tPGA (ms) when performing a grasping action to each type of cylinder (first object) in relation to the size (relative to the first cylinder's diameter) and orientation of the second object.*

	First Object:	
Second Object (size/orientation):	Cylinder (6cm)	Cylinder (5cm)
Larger/Left	552 (128)	519 (110)
Larger/Straight	556 (143)	517 (124)
Larger/Right	533 (136)	523 (129)
Same/Left	525 (123)	529 (143)
Same/Straight	539 (127)	515 (111)
Same/Right	544 (126)	539 (129)
Smaller/Left	547 (137)	525 (117)
Smaller/Straight	545 (132)	519 (123)
Smaller/Right	544 (132)	535 (134)

APPENDIX C: CHAPTER 4 (EXPERIMENT 3) DESCRIPTIVE STATISTICS

Table 12. *Mean PGA (mm) when performing a grasping action to each type of cylinder (first object) in relation to the size (relative to the first cylinder's diameter) and orientation of the second object, as well as the type of condition.*

		First Object:	
Condition:	**Second Object (size/orientation):**	Cylinder (6cm)	Cylinder (5cm)
Open-Loop	Larger/Left	76.75 (7.9)	74.25 (9.9)
	Larger/Straight	77.68 (7.6)	74.38 (8.1)
	Larger/Right	77.32 (9.4)	75.23 (9.5)
	Same/Left	78.48 (7.1)	72.05 (7.9)
	Same/Straight	77.10 (6.7)	73.97 (8.7)
	Same/Right	77.68 (7.9)	73.62 (7.8)
	Smaller/Left	76.91 (7.8)	74.08 (8.0)
	Smaller/Straight	78.21 (8.6)	73.64 (8.7)
	Smaller/Right	77.24 (8.4)	74.52 (9.0)
Closed-Loop	Larger/Left	77.18 (7.8)	73.59 (8.7)
	Larger/Straight	77.03 (6.6)	73.49 (8.4)
	Larger/Right	77.43 (7.8)	72.64 (7.6)
	Same/Left	78.25 (8.5)	73.62 (7.9)
	Same/Straight	76.99 (7.3)	73.31 (7.9)
	Same/Right	76.33 (7.4)	73.37 (8.1)
	Smaller/Left	76.89 (7.6)	72.72 (7.7)
	Smaller/Straight	76.91 (8.1)	73.67 (8.9)
	Smaller/Right	77.49 (7.3)	72.36 (8.3)

Table 13. *Mean grip orientation (degrees) when performing a grasping action to each type of cylinder (first object) in relation to the size (relative to the first cylinder's diameter) and orientation of the second object, as well as the type of condition.*

		First Object:	
Condition:	**Second Object (size/orientation):**	Cylinder (6cm)	Cylinder (5cm)
Open-Loop	Larger/Left	-5.14 (13.9)	-5.91 (14.6)
	Larger/Straight	-3.47 (11.7)	-3.18 (13.4)
	Larger/Right	-3.30 (12.1)	-2.77 (16.2)
	Same/Left	-4.14 (13.7)	-5.28 (13.9)
	Same/Straight	-4.05 (14.2)	-5.98 (12.3)
	Same/Right	-2.34 (13.1)	-3.75 (15.4)
	Smaller/Left	-5.04 (13.9)	-4.28 (13.1)
	Smaller/Straight	-5.62 (13.4)	-3.57 (15.7)
	Smaller/Right	0.35 (13.6)	-3.25 (15.7)
Closed-Loop	Larger/Left	-3.53 (11.7)	-1.71 (13.0)
	Larger/Straight	-2.34 (12.3)	-1.09 (12.0)
	Larger/Right	-4.34 (11.4)	-3.14 (11.9)
	Same/Left	0.37 (11.9)	-3.82 (13.9)
	Same/Straight	-2.87 (12.1)	-3.42 (13.2)
	Same/Right	-2.15 (13.3)	-1.99 (12.1)
	Smaller/Left	-1.27 (13.8)	-3.01 (12.3)
	Smaller/Straight	-3.94 (13.1)	-1.47 (14.0)
	Smaller/Right	-2.11 (13.7)	3.63 (14.1)

Table 14. *RT (ms) when performing a grasping action to each type of cylinder (first object) in relation to the size (relative to the first cylinder's diameter) and orientation of the second object, as well as the type of condition.*

		First Object:	
Condition:	**Second Object (size/orientation):**	Cylinder (6cm)	Cylinder (5cm)
Open-Loop	Larger/Left	539 (322)	530 (330)
	Larger/Straight	503 (281)	509 (331)
	Larger/Right	485 (280)	520 (300)
	Same/Left	519 (309)	483 (244)
	Same/Straight	489 (291)	472 (253)
	Same/Right	496 (292)	515 (318)
	Smaller/Left	473 (252)	527 (324)
	Smaller/Straight	451 (220)	501 (267)
	Smaller/Right	470 (253)	486 (329)
Closed-Loop	Larger/Left	505 (222)	492 (269)
	Larger/Straight	479 (162)	520 (280)
	Larger/Right	544 (305)	495 (254)
	Same/Left	488 (260)	482 (245)
	Same/Straight	472 (197)	475 (223)
	Same/Right	509 (237)	530 (284)
	Smaller/Left	483 (192)	499 (263)
	Smaller/Straight	538 (233)	517 (259)
	Smaller/Right	514 (245)	471 (256)

Table 15. *MT (ms) when performing a grasping action to each type of cylinder (first object) in relation to the size (relative to the first cylinder's diameter) and orientation of the second object, as well as the type of condition.*

		First Object:	
Condition:	**Second Object (size/orientation):**	Cylinder (6cm)	Cylinder (5cm)
Open-Loop	Larger/Left	413 (90)	423 (84)
	Larger/Straight	409 (94)	413 (71)
	Larger/Right	415 (83)	417 (92)
	Same/Left	413 (92)	413 (118)
	Same/Straight	423 (94)	415 (81)
	Same/Right	424 (94)	404 (93)
	Smaller/Left	414 (86)	411 (85)
	Smaller/Straight	404 (72)	407 (96)
	Smaller/Right	424 (102)	428 (83)
Closed-Loop	Larger/Left	451 (82)	451 (85)
	Larger/Straight	434 (85)	434 (77)
	Larger/Right	436 (88)	445 (98)
	Same/Left	441 (90)	444 (85)
	Same/Straight	445 (93)	441 (86)
	Same/Right	446 (88)	428 (83)
	Smaller/Left	439 (87)	455 (94)
	Smaller/Straight	432 (66)	441 (85)
	Smaller/Right	467 (81)	422 (83)

Table 16. *tPGA (ms) when performing a grasping action to each type of cylinder (first object) in relation to the size (relative to the first cylinder's diameter) and orientation of the second object, as well as the type of condition.*

Condition:	**Second Object (size/orientation):**	**First Object:** Cylinder (6cm)	Cylinder (5cm)
Open-Loop	Larger/Left	234 (90)	229 (96)
	Larger/Straight	249 (96)	240 (92)
	Larger/Right	245 (97)	231 (103)
	Same/Left	230 (95)	237 (101)
	Same/Straight	236 (91)	220 (100)
	Same/Right	238 (85)	236 (96)
	Smaller/Left	240 (109)	226 (89)
	Smaller/Straight	228 (91)	218 (89)
	Smaller/Right	213 (82)	235 (95)
Closed-Loop	Larger/Left	272 (104)	275 (110)
	Larger/Straight	253 (100)	260 (102)
	Larger/Right	263 (98)	274 (111)
	Same/Left	259 (105)	280 (106)
	Same/Straight	279 (102)	265 (111)
	Same/Right	279 (101)	259 (102)
	Smaller/Left	264 (107)	278 (983)
	Smaller/Straight	258 (116)	264 (103)
	Smaller/Right	295 (102)	253 (92)

APPENDIX D: CHAPTER 5 (EXPERIMENT 4) DESCRIPTIVE STATISTICS

Table 17. *Mean grip orientation (degrees) when grasping a cylinder (first object) in relation to the orientation of the second object for each type of condition.*

	Condition:	
Orientation of Second Object:	Easy	Difficult
Left	-3.63 (8.1)	-3.97 (8.2)
Straight	-3.32 (8.2)	-2.93 (8.0)
Right	-3.88 (8.9)	-3.05 (8.1)

Table 18. *RT (ms) when grasping a cylinder (first object) in relation to the orientation of the second object for each type of condition.*

	Condition:	
Orientation of Second Object:	Easy	Difficult
Left	351 (72)	359 (100)
Straight	340 (89)	357 (94)
Right	347 (78)	356 (79)

Table 19. *MT (ms) when grasping a cylinder (first object) in relation to the orientation of the second object for each type of condition.*

	Condition:	
Orientation of Second Object:	Easy	Difficult
Left	517 (71)	526 (87)
Straight	513 (77)	527 (74)
Right	517 (68)	538 (88)

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