VISUAL INTERACTION WITH AMBIGUOUS EDGES:

PERCEPTION, POINTING AND PREHENSION

by

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Abstract

The current investigation examined perceptual and movement responses to evaluate the possibility of unique representations guiding the outcomes of perceptual and motor-based responses. In two experiments the quality of visual luminance edges was manipulated and the outcomes of three visually based tasks, namely perceptual estimates, pointing, and prehensile/grasping movements were measured. The findings provided evidence for the use of unique representations of stimulus features that are task specific.

Preface

Both of the experiments included in sections 2.3 and 2.4 were completed under the approval the the University of British Columbia Okanagan Behavioural Research Ethics Board (Cert #H07-01734).

The research in section 2.3 was born under the direction of Dr Gordon Binsted of the Sensorimotor Neuroscience Laboratory at the University of British Columbia Okanagan campus. The initial research question and a general notion of how to go about it was suggested by Dr Binsted. We collaborated upon the specific design of the experiment, and I was responsible for the programming, collection, and analysis of data.

The research in section 2.4 was inspired by the results of the first experiment. Collaboration between myself and Dr Binsted was undertaken in the designing of the second experiment, but I was afforded significantly more control over many of the specifics of the methods and stimuli.

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To Christina, The Love of my Life

Chapter 1: Introduction

1.1 *General Background*

The human visual system is comprised of a vast array of neural connections tasked with making sense of the ever-complicated visual world in which we live. In doing so, it must process two fundamental properties of the light received by the eyes: intensity (brightness), and wavelength (colour) (Carlson, 2007). As an example, consider the simple act of picking up a mug of coffee. Initially, the visual system is required to detect the presence of a stimulus and determine the spatial extent of the object as determined by its boundaries. The visual system can then use this information to guide one's hand to grasp the mug (i.e., prehension). Paradoxically, the visual subsystem that mediates the control of such goal-directed action is unavailable to conscious awareness. The visual system can further process the features of the mug to extract overt estimates of size, shape, texture and colour can be used to establish object identity. These perceptual estimates reflect the overt conscious judgements about a particular stimulus set (Prablanc & Martin, 1992). The following section explores the historical and current evidence in favour of this functional segregation between perception and action within the human visual system.

1.2 *The Two Visual Streams of Human Vision*

The human visual system consists of a vast array of connections originating at the retina and terminating in areas all over the cerebral cortex. Early work on the organization of the human visual system revealed that the neural signals processed at the level of the V1 (primary visual cortex in the occipital lobe) which originated at the retina, travel to the cortex through the thalamus. The transition of processing to the cortex through the thalamus is common to other sensory modalities including audition (Kaas & Hackett, 2000**)**. Specifically, visual information

travelled primarily through the lateral geniculate nucleus of the thalamus (LGN) (Weiskrantz, 1996).In 1968, Hubel and Wiesel presented seminal work examining the visual specialization of cortical areas in both a cat and a nonhuman primate. The authors identified specific cortical cells responsible for the processing of visual stimulus features in the occipital cortex area now widely referred to as primary visual cortex (V1). Notably, humans who suffer brain damage in V1 report no visual experience at all and their deficit has become known as cortical blindness (Weiskrantz, 1996). In addition, profound visual deficits are also associated with lesions to areas other than the occipital cortex. For instance, individuals with damage to the temporal cortex may exhibit visual deficits known collectively as agnosias (Milner & Goodale, 1995), which are characterized by the inability to identify visual stimuli. Depending upon the specific cortical area and severity of the damage, the deficit can range from prosopagnosia (the inability to recognize faces) to visual-form agnosia (the inability to recognize visual objects all together) (Kandel & Wurtz, 2000; Milner & Goodale, 1995). Individuals with damage to the posterior parietal cortex may produce deficits such as spatial neglect, which is characterized by a failure to attend to a region of visual space (Vallar, 2001), or optic ataxia, which is characterized by a failure to interact with objects even though they can be verbally identified (Milner, Dijkerman, McIntosh, Rossetti, & Pisella, 2003). Damage to the temporal-parietal junction, may exhibit a deficit in detecting the motion of objects (Rizzo, Nawrot, & Zihl, 1995). Together, these deficits suggest that the cortical processing of visual information operates across multiple, physically separate and functionally distinct areas, and that a complete understanding of how the visual system works as a whole requires the consideration of its constituent parts.

Inter-connectivity patterns of the constituent parts of the visual system beyond V1 (i.e., extra-striate areas) were mapped and yielded two primary projections : one system that extends

dorsally and terminated in posterior parietal cortical regions (PPC), while the other extended

ventrally and terminates in inferior temporal (IT) regions (Ungerleider & Mishkin, 1982). Not

coincidentally, the general locations to which these primary projections extended overlapped with

the regions which, when damaged, yield specific and predictable visual deficits. In particular,

damage to the ventral projections within the temporal cortex matched those with visual agnosia

and the system was dubbed the 'what' pathway (Mishkin, Ungerleider & Macko, 1983). Damage

to the dorsal projections within the PPC which included those areas within the dorsal pathway,

led to individuals which spatial deficits such as poor relative localization skills (Pohl, 1973) and

unilateral spatial neglect (Vallar, 2001). The system was therefore dubbed the 'where' pathway.

Thus the human visual system appeared to be organized beyond V1 into two visual streams of

connections (See Figure 1.1). Although well founded in neuroanatomical examinations of

nonhuman primates, the two visual stream model forward by Ungerleider and Mishkin (1982)

was subsequently modified to accommodate clinical findings. Specifically, Patient DF suffered

extensive bilateral damage to the lateral occipital complex (LOC) in her inferior temporal cortex

(Goodale, Milner Jakobson, & Carey, 1991). This ventral stream damage (the 'what' pathway)

resulted in severe visual-form agnosia. DF could not identify objects presented to her or provide

their dimensions. However, DF could accurately manipulate and interact with the objects

presented to her. Conversely, patient AT suffered PPC damage resulting in optic ataxia (Milner et

al., 2003). AT could correctly identify objects and their dimensions, but could not accurately

manipulate or interact with them. The deficits suffered by DF fit with the notion that her

ventral/what stream had been damaged. AT, on the other hand, suffered damage to the

dorsal/where stream and lost the ability to accurately interact with objects, but remarkably

retained the ability to verbally localize them. Thus branding the dorsal stream as the 'where'

DORSAL STREAM: "WHERE"

PPC

V1

IT
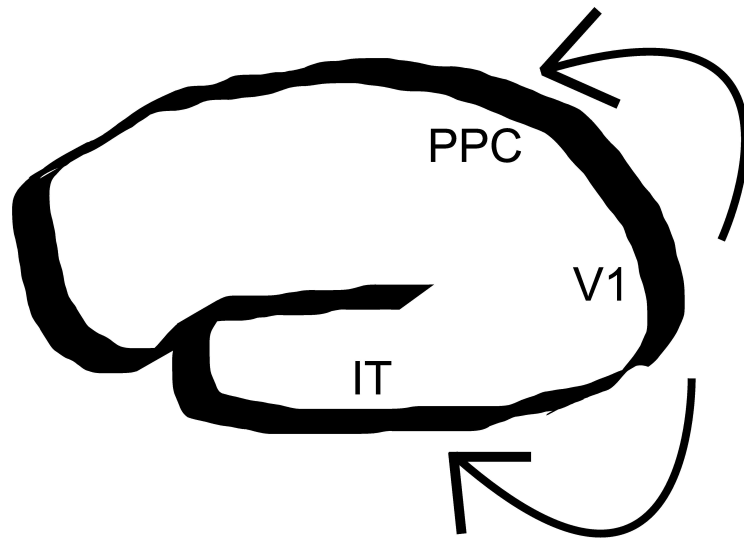
VENTRAL STREAM "WHAT"

Figure 1.1: The dual visual stream model of human vision.. Ungerleider and Mishkin (1980) described physiological connectivity between primary visual areas (V1 in the occipital cortex) and dorsal extrastriate visual areas (PPC) and ventral extrastriate visual areas (IT cortex). Based on the literature of the time, it was concluded that the dorsal stream functioned to represent the spatial location of stimuli whereas the ventral stream functioned to identify the stimuli.

stream of human vision appeared inappropriate as a deficit in localization manifested itself during motor interactions, but not overt judgements. The existence of the double dissociation of deficits

between DF and AT resulted in a rebranding of the ventral (what) stream as the ventral (vision-for-perception) stream, and the dorsal (where) stream as the dorsal (vision-for-action) stream. Milner and Goodale's (1995) proposed the rebranding as a new model called the Perception-Action two visual streams model of human vision.

Perceptual-cortical blindness associated with damage to primary visual cortex has also developed as an important source of information for understanding the dual visual stream model. Although individuals report no conscious experience in their blind visual field, some individuals exhibited "blindsight," and have reported the presence of stimuli located there at better than chance levels (Weiskrantz, 1996). Unfortunately, until an equivalent phenomenon to blindsight in non-lesioned individuals was discovered, one could not determine if the retained ability in blindsight was simply an adaptation to injury or evidence of normally functioning neural pathways. In a recent examination by Ro (2008), transcranial magnetic stimulation (TMS) was used to create a temporary blind spot or scotoma in V1 of normal individuals. Individuals performed quite well when tasked with interacting with stimuli placed within their temporary scotoma despite having no conscious experience of the stimulus. This finding indicated that alternative channels of neural processing function in normal individuals. Thus, the visual information must have arrived at dorsal stream areas via a route other than the LGN-V1-PPC pathway, with one possible route including the superior colliculus and pulvinar nucleus of the thalamus (Goodale & Westwood, 2004). Moreover, the lack of a conscious percept indicated that the ventral stream may not benefit from similar multiple pathways (Weiskrantz, 1996).

Although the Perception-Action model of human visual system functioning has strong foundations in findings from individuals who suffered brain damage, an important extension has been the finding of support in normal individuals. A useful way to test the model is to generate

scenarios where either the perceptual system (ventral stream) or the visuomotor system (dorsal stream) are selectively biased. Visual illusions are by their very nature an attempt to distort perceptual experience and therefore are a convenient method to bias the perceptual system (see Ramachandran & Ramachandran, 2008). The visual illusions of most interest are simple and generally related to size or orientation, as these properties are relevant to visuomotor tasks. Importantly, if visual illusions produce dissociations between perception and action, then the case for the Perception-Action model of human visual functioning would be strengthened.

An early and often cited experiment has involved the Ebbinghaus illusion where the perceived size of a disc is modulated by the relative size of surrounding discs. The larger the surrounding discs, the smaller the perceived size of the central disc and vice versa. Although perceptual estimates of size of the central disc were significantly modulated by the different sizes of the surrounding discs, maximum-grip-aperture (MGA) scaled consistently to the actual size of the central disc (Aglioti, DeSouza & Goodale, 1995). Thus the ventral system is apparently biased by the illusion whereas the action/dorsal system is not, providing evidence for a dissociation between perception and action existing in individuals not suffering from brain lesions.

The complete resistance of the dorsal stream to perceptually biasing visual illusions has come into question through the examination of visual illusions other than the Ebbinghaus illusion. For example Daprati and Gentilucci (1997) examined perceptual estimates of size and grasping responses to the Muller-Lyer Illusion. The Muller-Lyer illusion biases judgements of length of a line by adding fins to the end of a line (imagine a > < or < >). If the fins extend out beyond the line (fins out configuration), the line is perceived as being longer than a comparable line with the fins extending inward (fins in configuration). Daprati and Gentilucci (1997) found

the expected perceptual biases due to the illusion, but also a small effect of the illusion on MGA. The performance of MGA was explained as a two stage process with the motor system initially processing the stimuli as a whole (including the biasing fins) which would result in biased estimates, and a second stage of processing where the absolute distance of the stimulus to the hand is computed and monitored which would correct for the early bias. These findings were mirrored by Bruno and Franz (2009) who reviewed studies involving grasping and the Muller-Lyer illusion. They reported that MGA was always influenced by the illusion, but to a lesser degree than were perceptual estimates. They also reported that when responses were performed without continued vision of the stimulus (for a period of 2 s prior to making a response) under a no vision of stimulus during response (NVS) condition. In the NVS condition, the bias was found to increase due to the lack of availability of visual feedback. It was argued that the preparation of a grasping movement was likely to share a stimulus representation with perception, and biases could be overcome (partially) in grasping movement through the utilization of visually guided feedback.

The notion of the presence of a dissociations between perception and action in human vision was further tested in relation to both specific stimulus visual information and visual (stimulus viewing) conditions. For instance, under the normal or full vision of stimulus during response (FVS) condition, movements were generally unbiased by visual illusions, but movements became biased by illusions when vision of the biasing stimulus was removed prior to the initiation of the movement (Westwood & Goodale, 2003). It has been argued that the changes in the influence of illusions on movements across visual conditions are a consequence of perceptual representations biasing motor outcomes over time (Hu & Goodale, 2000). Additionally, the visual feature of colour has been demonstrated to be processed differentially

between the two visual streams. Perceptual tasks do not exhibit a pattern of differential performance on a localization task when the key stimulus feature varied was either brightness (luminance) or colour. Importantly, a relative decrement in performance was uncovered for the dorsal stream when coloured stimuli are used. Therefore colour-based stimulus features were found to be less salient to the dorsal/movement system compared to other stimulus features such as brightness (Cressman, Franks, Enns, & Chua, 2006)

One facet of the Milner & Goodale's (1995) dual-visual stream model of human vision that is often challenged is the idea that both the dorsal and ventral visual streams receive visual information from early visual areas and generate unique spatial representations of the world. Bruno and Franz (2009) recently reviewed the dual visual stream literature and sub-divided the competing perspectives into five views based on the degree of inter-relatedness of the spatial representation between the two visual streams. For the purposes of the current investigation the five views proposed by Bruno and Franz (2009) have been further condensed into three competing models:

1. The first model is the Perception-Action model of Milner and Goodale (1995). This model predicts the existence of unique representations between perception and action. It holds that only movements that are completed quickly and require visual guidance will rely upon a unique spatial representation (see Goodale & Westwood, 2004). NVS movements and slow movements will be governed by a more conscious and perceptual representation.

2. A second model, advocated by Bruno and Franz (2009), was dubbed the motor control hypothesis. Here the authors argue that a unitary representation could be shared between the streams and function through the presence and utilization of visual feedback to

accurately interact with the world. For the purposes of the current investigation this model will be referred to as the unitary representation model. The unitary representation could be biased as the perceptual report would indicate, but the motor response would utilize feedback to ensure the target was achieved regardless of the perceived representation of the stimuli. Under the Unitary Representation account, it has been argued that many previously measured dissociations between perception and action could be explained by specific task constraints placed upon either perceptual measures or motor-implied measures.

3. A final model on dual-visual stream organization in vision is known as the Planning and Control model (see Glover, 2004). In this model, ventral perceptual representation influence the planning of all movements, and dorsal/control representation influence the visual guidance during the later stages of goal-directed movements.

In counterpoint to Bruno and Franz (2009), Goodale and Westwood (2004) noted that a single spatial representation could not adequately explain double dissociations seen in individuals with brain lesions. They suggested the only way to reconcile this finding was to allow both visual streams to generate their own spatial representations. The degree to which the spatial representations of the two visual streams are similar, separate, or shared remains an area of interest in the literature.

1.3 *Use of Stimulus Features to Study the Two Visual Streams*

Visual stimuli can vary in many different ways including size, colour, texture, brightness, and shape. The ability to completely represent a stimulus requires the computation and knowledge of each of these relevant properties. The properties themselves can be described

further with specific attributes, or features. For instance, brightness can be measured as a function of luminance, and colour can be measured as a function of wavelength. The entirety of a stimulus can then be described as a combination or a set of property-defining stimulus features. To investigate the degree of similarity in the spatial representations utilized across the two visual streams, a single relevant stimulus feature can be varied. One stimulus property important to both overt perceptions (ventral-stream) and visually guided behaviours (dorsal-stream) is the size of a given stimulus which can be determined by the spatial extent enclosed by its edges. Edges therefore, can be interpreted as an important stimulus feature since they help to define geometric form and size.

Visual edges also come in many forms and to simplify the investigation, a single type of edge would have to be chosen. Edges can be defined by changes in luminance (brightness), texture (changes in patterning on the surface of the stimulus), wavelength (colour), or movement (uniform and between multiple items) (Enns, 2004). A chosen edge-type for manipulation and experimentation would have to fulfil two basic criteria. First, the edge type would have to be manipulable to varying degrees in a linear fashion. Second, the edge-type could not have any known preferential decrements or biases between perception and action. The first criterion eliminates the inclusion of both movement-edges and texture-based edges, because changing the quality of a movement edge could have significant influence on not only the quantifiable size of a stimulus, but also its shape, and increasing the similarity in texture between a stimulus and its background may result in a failure to influence perceived size while also decreasing detectability (Reagan & Hong, 1994). The second criterion eliminated colour-based edges given that chromaticity has been found to differentially influence movement-based responses and perceptual reports to the same stimuli (Cressman et al., 2006). Fortunately, luminance-based edges, satisfy

the required criteria because the luminance of a given area can be easily manipulated over space as it is a scalar value, and has not been found to disadvantage either perception or action (Cressman et al., 2006). Furthermore, luminance edges are processed early at the cortical level (V1), that is prior to major bifurcation into the two visual streams (Hubel & Wiesel, 1968).

Before using luminance-based stimuli as a tool for comparing the outcomes of perception and action, one must consider the influence of variations in the quality of the luminance-based edges which bind luminance-based stimuli. Specifically, visual detection can be thought of as an important step in the accurate utilization of visual information. However, the detectability of luminance-based stimuli can be systematically influenced by many factors. Some important factors include size, shape/symmetry, spatial frequency, ambiguity of the edges, and contrast. Luminance-based stimuli show increased detectability as a function of size, initially increasing with size monotonically then asymptotically levelling off for yet increasingly larger sizes (Adrian, 1989; Bijl, Koenderink & Toet, 1989, Lamar, Hech, Shlaer, & Hendley, 1947; Shapely, 1974). Similarly, symmetrical luminance-based stimuli are easier to detect than asymmetrical stimuli (Bijl & Koenderink, 1993; Lamar et al., 1947). The spatial frequencies of luminance-based stimuli have been manipulated through the utilization of rectilinear sine-wave gratings (vary in one dimension), circular sine-wave gratings (vary in two dimensions), and bessel stimuli (vary in two dimensions) (Kelly & Magnuski, 1975). All stimuli exhibited increases in detectability up to the point where the stimulus became increasingly more difficult to define. The influence of edge-ambiguity has also been examined with increasing size of Gaussian luminance blobs. Increases in size were systematically linked to increases in edge-ambiguity. Both increases were linked to increases in detectability up to a point, which then levelled off and subsequently decreased in detectability (Shapley, 1974). The last property to exert influence on detectability

considered is contrast. Contrast can measured as the difference in brightness between a stimulus and its background (Enns, 2004). Increases in contrast have been found to decrease perceptual latencies to stimuli, and therefore decrease detection thresholds (Lupp, Hauske, & Wolf, 1976).

A subsequent but equally important step in the accurate utilization of visual information is the precise localization of the detected stimulus and its visual features. Stimulus features relevant to their detection can be important in their localization as well. Regarding this notion, Wilcox and colleagues (Wilcox, Elder & Hess, 2000) examined the influence of two stimulus features on accurate localization: stimulus size and the ambiguity of the edges. The authors anticipated the blurring of the edge of a stimulus would result in differences in judgement of perceived size. Given that location judgements were the measure of interest, the sizes of the circle stimuli (blurred edges) were equated experientially (perceived target size) rather than physically (actual target size) with the Gaussian stimuli. Only the greatest degree of blurring influenced the perceptual judgements; estimations across size and blur revealed that increasing edge blur and increasing size both reduced localization performance. The findings suggested that the higher the frequency information available to the visual system, the more accurate the localization an estimate. A sharp non-blurred edge encompasses a relatively large amount of high frequency information, while increasing blur results in the degradation of this high frequency information and thus decreases in localization ability.

To accurately localize a stimulus in space, one must also accurately identify the spatial extent of the stimulus. This can be accomplished in a general way by defining the location of the boundaries or edges of the stimulus in question. If the edge of a stimulus is difficult to identify, then the size of the stimulus should in turn, also be difficult to identify. For example, Fredericksen, Bex, and Verstaten (1997) investigated the perceived size of dynamic sinusoidal

gratings that were windowed in a Gaussian-envelope. Given that the windows were Gaussian in nature, increases in window size corresponded with an increasing edge-blur or edge-ambiguity. The edge of the Gaussian windows were expected be difficult to localize due to the gradual decays, and thus it would be reasonable to expect that difficulty localizing edges would yield more variable estimates of location. Contrary to this expectation, size estimates were very consistent. Thus, although the location of the edge appeared ambiguous, the location of the edge determined by the visual system was highly consistent.

When considering the determination and localization of edges, blurred or otherwise, two major models need to be considered. The models include the peaks in local energy model (Marrone & Burr, 1988), and the zero-crossings in the second derivative of the intensity profile model (Marr & Hildreth, 1980). The peaks in local energy model describe a possible means for localizing the visual features of edges and lines. Features are analyzed by first taking the Fourier transform of the luminance profile. Visual features can then be localized by examining areas where either the peaks of the component sine waves lined up (for edges), or the peaks in the component cosine waves lined up (for lines) (Marrone & Burr, 1988). Second-derivative models describe the localization of edges at locations of zero-crossings in the second derivative of the luminance profile. Whenever a change in luminance occurs across a distance, a gradient exists between the two corresponding levels of luminance. The steepest point in the luminance gradient is where the edge can be localized. The edge location can also be represented in the first derivative of the luminance profile as either a maxima or a minima (depending on the direction of change of the edge), but in the second derivative it always occurs at a zero crossing (Marr & Hildreth, 1980) (See Figure 1.2). In a recent examination of these models, Hesse and Georgeson (2005) employed an edge localization task and built visual stimuli which exhibited a single peak

in local energy (representing a line). They determined that the peak in local energy peak model fit poorly with their findings as edge features were consistently localized where no peaks in local energy had occurred (Experiment 1). They also employed an alignment task (Experiment 2) where the task was to judge the relative location of a blurred bar that had been shifted relative to two other reference bars (above and below). While the peak in local energy model was an adequate predictor of the alignment task at low levels of blur, the location judgements became more inaccurate with increasing blur. Conversely, the second-derivative model yielded more accurate predictions across all levels of blur. Thus the locations of the zero-crossings in the second derivative of the luminance profile may yield important relevant stimulus information (Marr & Hildreth, 1980).

While informative, the previously discussed findings are derived solely from perceptual judgements. To perform an accurate motor-based task with a physical stimulus, presumably the dorsal stream must detect, localize, and process relevant stimulus features such as size and shape. In a novel study, Gegenfurtner and Franz (2007) investigated the relationship between the perceived relative location of an object and the endpoint-implied location of pointing movements. Critically, the authors made a notable attempt to generate directly comparable measures of overt visual perception (ventral stream) and motor action outputs (dorsal stream). Two tasks were employed to assess the relative location of a Gaussian blob (i.e., a 2D Gaussian luminance distribution): a forced choice perceptual report task and a manual pointing task. While the reported direction of estimated location was highly correlated across the perception and action tasks for any given location, the accuracy of the perceptual judgements was greater as measured by a steeper slope in the psychometric function. The authors concluded that due to the large agreement across both conditions and participants, perception and action likely shared at least
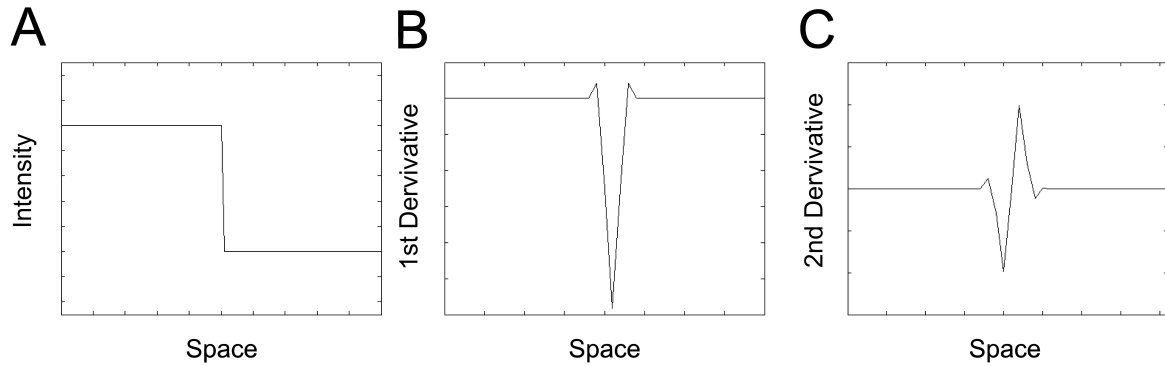
Figure 1.2: A second-derivative representation for edge-detection. (A) The luminance profile of a sharp edge. (B) The first derivative of A. (C) The second derivative of A. Note a zero-crossing in C coincided with the drop in luminance level in A. (Adapted from Marr and Hildreth, 1980).

similar processing mechanisms, and possibly a shared representation of stimulus location. By corollary, it could be inferred that the ventral (perceptual) stream and dorsal (motor-based) stream could share a representation of the location of edges.

1.4 *Research Question*

The present research addressed the following question: How do the two visual streams represent early processed visual features? The representation of early processed visual features was expected to exist as either a unitary representation, between the two visual streams or unique representations between them. An early processed visual feature is operationally defined as a feature processed prior to the bifurcation into two visual streams. Luminance edges were chosen as the feature to be manipulated as their processing occurs in cortical visual areas as early as V1 (Hubel & Wiesel, 1968; Milner & Goodale, 1995). Moreover, luminance edges help to define

form, and visual form is an important piece of information for both identification of a stimulus and accurate visuomotor interaction with the stimulus. The representation of luminance edges was assessed through the analysis of the measurable outcomes of the two visual streams, namely overt perceptual estimates (ventral stream), and motor-implied estimates (dorsal stream).

1.5 *Hypotheses*

Physiological edge-detectors have been localized to cortically early visual areas such as V1 (Hubel & Wiesel, 1968), and therefore the initial hypothesis was that the two visual streams of human vision would share the same representation of edge location This expectation was driven by the previous findings of Dyde and Milner (2002) who reported the existence of a visual illusion which biased both perception and action and concluded that the visual information had been processed sufficiently early to be common to both streams. If both visual streams received comparable feature information of the edges, then both ventral and dorsal estimations of luminance edge location would be predicted to be equivalent.

Thus it was predicted that the influence of ambiguous edges on perceptual and motor responses would be equivalent across tasks. More specifically, the scaling of perceptual and motor-based responses to ambiguous edges would be expected to be equivalent both across different levels of blur (ambiguity), and across different levels of stimulus size within a level of blur. In terms of the three competing models of human vision considered within the current investigation, all three, namely the Perception-Action model, the Planning and Control model, and the unitary representation model predict a comparable influence of increasing edge ambiguity on both perceptual and motor-based outcomes.

As some of the strongest evidence for dissociations between perception and action have come from studies using NVS responses, and thus such as response was included in Experiment

2. The inclusion of a NVS task has previously been found to result in perceptual estimates scaling more similarly to motor-based responses (Hu & Goodale, 2000). Under this scenario, it was predicted that because the ambiguous edge information would be common to both before the removal of a stimulus from view (for the purposes of a NVS response), a delay would not result in a differential pattern of results between perception and action. While all of the considered models supported this hypothesis, the models which allowed for unique stimulus representations to exist across the human visual system (Perception-Action and Planning and Control) could also explain a situation where NVS responses differed between perception and action. Differences could be explained because under these models perceptual stimulus representations are believed to be much more resistant to decay in a NVS condition while motor-based (dorsal) representation are expected to exist relatively transiently (Westwood & Goodale, 2003).

Chapter 2: Experiments

2.1 *General Approach*

The core approach used in these experiments was psychophysical. Two outcomes of the ventral and dorsal streams were discretely measured and compared: ventral stream function was inferred from overt perceptual responses (i.e., self-report), while dorsal stream performance was attained through the measurement of visually-guided movements (i.e., kinematics). The control of movements by the dorsal-stream has been found to be generally non-conscious in nature (Goodale, Pellison & Prablanc, 1986). Measures attained through the analysis of movement parameters resulted in implied estimates, as an overt estimation would require perceptual, and therefore ventral estimations.

2.2 *General Methods*

Both experiments were controlled using custom in-house MATLAB scripts in conjunction with the Psychophysics Toolbox 3.0 (Brainard, 1997). The scripts randomized condition selection, controlled the trial sequences, and saved the experimental data. Reaction time (RT) was defined as the time in milliseconds (ms) from the presentation of the go-signal to the initiation of the response by the participant. Movement time (MT) was defined as the time following the initiation of a movement required by the participant to complete the movement. Error trials were screened online (i.e., prior to next trial) and removed if RT or MT exceeded normal bounds (task dependent: e.g., $150 < RT < 500$ msec, $300 < MT < 800$). Error trials were re-randomized into the trials-to-be-run list. An Optotrak System (Optotrak 3020, Northern Digital Inc, Waterloo, ON) was used to track the three-dimensional (3D) positions of infrared-light-emitting diodes (IREDs) across time. In all cases, IREDs were digitized at 200 Hz, and the subsequent displacement data was filtered using a second-order dual-pass Butterworth filter (15

Hz, low pass). The IREDs were strategically placed either upon the hand of the participant, or upon a relevant experimental manipulandum to gather size estimates from participants. Each experiment consisted primarily of two tasks: a perceptual-estimate, and a goal-directed-movement which yielded a measurable motor-implied estimate. The perceptual-estimation tasks required participants to match the apparent size of a stimulus to estimate its size. Participants were instructed to be as accurate as possible and to take as much time as necessary. The goal-directed-movement task required participants to complete a required movement as-quickly-and-accurately-as-possible.

Stimuli within both experiments were generated with MATLAB scripts on a pixel-by-pixel basis. Both the size and the ambiguity of the edges of stimuli were manipulated within the experiments. The edges of the stimuli were made ambiguous with the utilization of a 2D Gaussian-distribution. All stimulus images generated were stored as .jpeg image files.

2.3 *Experiment 1: Perception and Pointing at Gaussian Blobs*

2.3.1 *Introduction*

Both the ventral and dorsal streams are generally reported to receive their inputs primarily from early visual areas such as geniculostriate connections (Ungerleider & Mishkin, 1982). The dorsal stream, ignoring extrageniculate pathways, passes from V1 through areas such as V2, V3 dorsal, middle temporal (MT), and the parieto-occipital area (PO) to areas such as the middle superior temporal (MST), ventral intraparietal sulcus (VIP) and lateral intraparietal sulcus (LIP). The ventral stream is believed to pass from V1 through areas such as V2, V3v, V4, and terminating in the inferior temporal area (IT). Significant dissociation in connectivity between the two visual streams occurs following information getting to area V2. V2 sends projections to areas V1, V3, V4, MT, and at greater than 30° eccentricities (of visual angle away from the

fovea), areas MST and VIP (Gattass, Sousa, Mishkin & Ungerleider, 1997). Recent findings

suggested that under specific conditions the parietal dorsal structures (e.g., intraparietal sulcus,

superior parietal lobule) can receive significant inputs from the tectum/superior colliculus,

(Cowey & Stoerig, 1991) and possibly the pulvinar nucleus of the thalamus (Rodman, Gross, &

Albright, 1989; Milner & Goodale, 1995). However, the evidence for alternative pathways was

obtained under situations when processing at V1 was not functioning normally, as the result of

temporary or permanent lesions (Ro, 2008; Weiskrantz, 1996). Therefore it is difficult to

conclude that such alternative pathways contribute significantly to the normal functioning of the

visual system. Also, while it was once proposed that a strong association existed between

ventral/dorsal and the parvocellular (P)/magnocellular (M) pathways from LGN respectively

(Livingstone & Hubel, 1988; Maunsell, Nealy, & DePriest, 1990), more recent evidence suggests

both visual streams receive integrated P and M inputs from V1 (e.g., regarding contrast-based

information see Allison , Melzer, Ding, Bonds,& Casagrande, 2000).

While many visual characteristics appear to be preferentially associated with each visual

stream (e.g., motion/dorsal, colour/ventral), the accurate localization of visual edges is an

important process to both the identification of and functional interaction with an object. As yet,

owing largely to the psychophysical (overt perceptual) nature of most investigations of edge-

detection (Hesse & Georgeson, 2005), comparable motor-based responses have often been

neglected (see Gegenfurtner & Franz, 2007 for an exception). The evaluation of perceptually-

based psychophysical principles such as Weber's Law from a motor-implied paradigm have only

recently been undertaken (Ganel, Chajut, & Algom, 2008). The current research helped improve

this discrepancy and evaluated the representation of luminance edges by varying their level of

ambiguity in both a perceptual and motor-implied paradigms. As blurring has been previously

found to influence both detectability and localization, it was hypothesized that stimuli with a 2D Gaussian luminance profile would appear smaller than stimuli of equated size represented as solid (square wave) circles.

2.3.2 *Materials and Methods*

    2.3.2.1 *Participants.*

    Twelve university-aged individuals (8 male, 4 female, mean age = 22.25 years) were recruited and participated in the current study. All participants were right handed (by self-report) and had normal or corrected-to-normal vision. Informed written consent was given by all participants before commencement of the study.

    2.3.2.2 *Apparatus.*

    Participants were seated facing a Plexiglas screen (30° incline away from the vertical plane). Stimuli were displayed upon the screen via a short throw projector (NEC VT-465) projecting a 1024 by 768 pixel image resulting in a 33 x 25 cm functional image size. Two different types of trials were completed: perceptual-estimation and pointing movements. Two IREDs were attached to opposing sides of a Lafayette anthropometric calliper (Model 01291) to record perceptual-estimation trials. An IRED was attached to the tip of each participant's right index finger for tracking pointing movements.

    2.3.2.3 *Stimuli.*

    Two different sets of stimuli were presented during the study: 2D Gaussian blobs and solid circles (See Figure 2.1). All stimulus images were generated such that luminance varied from 1 (white) to 0 (black). The sizes of Gaussian stimuli were manipulated by varying their 2D standard deviation (SD). All stimuli were mounted centrally upon a black 1024 by 768 pixel background. Each stimulus set was generated in five sizes (Gaussians with: SDs of 15, 25, 35, 45,

60 pixels yielding diameters of 2.5, 4.6, 6.3, 8.1 and 10.8 cm respectively; Circles with: diameters of 1.5, 2.1, 3, 4, and 5 cm respectively). As the perceived size of the Gaussian blobs was expected to be influenced by the degree of ambiguity, the sizes of circle stimuli was chosen to appear comparable to the apparent sizes of the Gaussian blobs (see Wilcox et al., 2000 for a similar manipulation of equating sizes). The actual sizes of the stimuli were calculated as the number of pixels across the diameter into which a value greater than zero was found. The pixel distance was then converted into centimetres using the known resolution (1024 by 768 pixels) and size of the display (33 by 25 cm).

2.3.2.4 *Procedures*.

Two experimental tasks were performed in 2 separate blocks of trials. One block was a perceptual-estimation task which required participants to estimate the width of a stimulus with a calliper. The other block was a pointing task which required participants to move the tip of their right index finger from the home position located 20 cm below the centre of the projected image to the location of a presented stimulus projected upon the screen. Regardless of task, trials began with the presentation of a stimulus which functioned as a go-signal, and in the pointing task an auditory tone accompanied the stimulus presentation. The primary measure in the pointing task was the motor-implied estimate of size defined as the effective target width (95% confidence interval [CI] of the endpoints in the primary movement axis, see Figure 2.2), as the endpoint spread of pointing movements have been found to scale with increases in stimulus size (Schmidt Zelaznik, Hawkins, Frank, & Quinn, 1979). Other movement related variables assessed included RT and MT. In the perceptual-estimation trials, the distance between the tips of the calliper after the participant was satisfied with the estimate was the primary measure. To facilitate a consistent

unbiased perceptual-estimations, participants were instructed to alternate on consecutive trials whether the calliper started in a fully-open or fully-closed position.
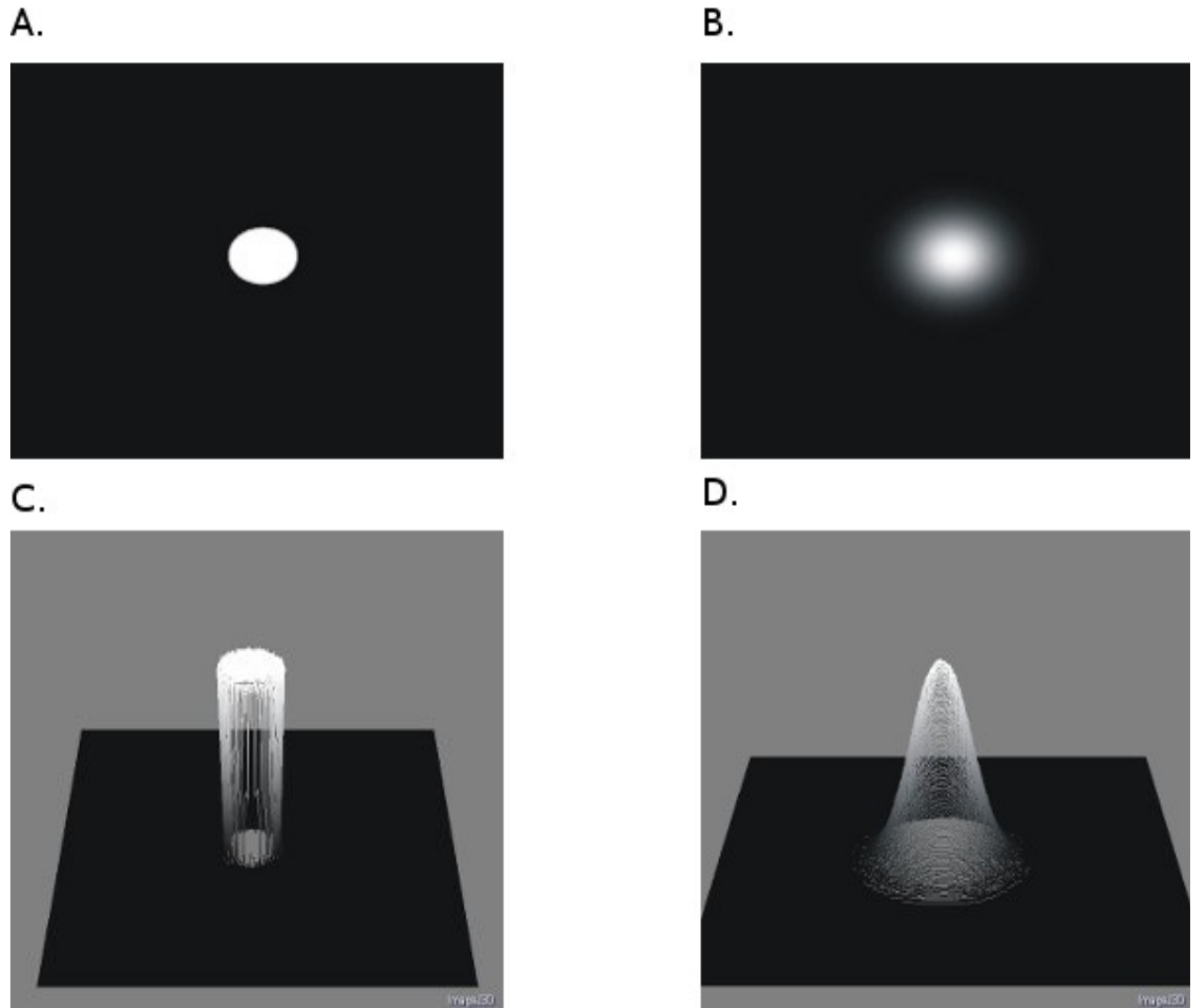
Figure 2.1: Examples of stimuli from Experiment 1. (A) circle, (B) Gaussian. (C) 3D representations of the luminance profile of the circle, (D) 3D representations of the luminance profile of the Gaussian. 3D plots generated with ImageJ software.

To protect against order effects, trial orders within a block were generated randomly by the computer, and half of the participants completed the pointing block first, whereas the other half completed the estimation block first. The pointing block consisted of 100 trials and the estimation block consisted of 50 trials. Each target stimulus was presented 10 times in the pointing block and five times in the perceptual block. Trial numbers were intentionally unbalanced due to the expectation that 95% CI movement endpoint estimates would be more variable than perceptual judgements, requiring more pointing trials to yield stable performance estimates.

Figure 2.2: Effective target width of pointing movements from Experiment 1. The movement-implied motor estimates of width were computed as the 95% CI of the movement end-points in the primary movement axis.

2.3.2.5 *Design and Analysis.*

To evaluate the relationship between estimated size and actual size between stimulus classes, paired-samples *t*-tests were run on the slopes of the relationship within a task. This was necessary because, the levels of size between stimulus classes were not precisely equivalent giv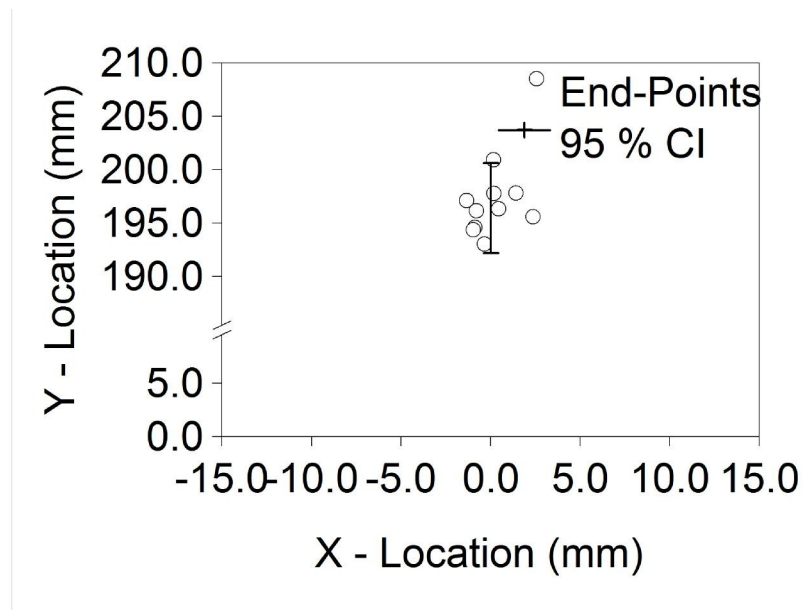en that they were based on an initial visual estimate. Therefore, the best comparison of the influence of increasing size of the stimuli was the rate of scaling of estimates to veridical increases in size. Further, the two *t*-test comparisons were assessed following the implementation of a Bonferroni correction for multiple comparisons at an alpha level of .05. As the rate-of-scaling between perceptual and motor-based tasks was not expected to be equivalent, comparisons were only made between classes of stimuli, and not between tasks (Franz et al., 2000; Smeets & Brenner, 1999).

2.3.3 *Results and Discussion*

2.3.3.1 *Confirmatory Analysis.*

Perceptual estimates of width scaled in a linear fashion with increasing size for both stimulus types. Linear contrasts were used to assess the linearity of the scaling of perceptual estimates to changes in stimulus size of both stimulus classes. The linear contrasts were significant for circles ($F(1,11) = 711.16$, $p < .001$, partial $\eta^2 = .98$) and Gaussians ($F(1,11) = 316.15$, $p < .001$, partial $\eta^2 = .97$).

In order to ensure the validity of the motor-implied estimates, behavioural data from the pointing trials was first assessed. The grand mean for RTs across all stimuli was 249 ms (SD = 9.65 ms). This value for RT fell within the previously reported bounds of 195 to 351 ms for a simple pointing movement with comparable stimuli (Gegenfurtner & Franz, 2007). MTs ($M = 449$ ms, SD = 13.07) decreased with increasing size of stimuli. The mean MT value also fell

within the expected range of values for comparable stimuli of 365 to 506 ms (Gegenfurtner &

Franz, 2007). The relationship between MT and stimulus size was assessed statistically by way of

linear contrasts for both stimulus classes. Linear contrasts were statistically significant for both

stimulus classes (circles: $F(1,11) = 15.11$, $p < .01$, partial $\eta^2 = .58$, Gaussians: $F(1,11) = 24.37$,

$p < .001$, partial $\eta^2 = .69$). Thus, as has been previously reported (Fitts, 1954), as the size of a

given target decreased, the MT of a pointing movement towards that target increased. The

general pattern of MT was consistent with a-priori expectations and was interpreted as evidence

that participants did follow instructions and performed the pointing movements as quickly and

accurately as possible. As the MT data revealed an expected pattern of scaling to changes in size,

the motor-implied estimates derived from the movements were deemed acceptable for further

analysis.

Recall that motor-implied estimates (i.e., effective target width estimates) were calculated

for movements as the 95% CI of the endpoints of the pointing movements in the primary

movement axis (see Figure 2.2). Mean motor-implied estimates were found to increase with

target size for both stimulus types (Figure 2.3).

2.3.3.2 *Slopes Analysis.*

Although the sizes of the circular stimuli were chosen to appear comparable in size to the

multiple sizes of Gaussian-blob stimuli, their actual/measured sizes were different. Due to the

ambiguous nature of the edges of the Gaussian-blob stimuli, circles of the same measured size

appeared much larger. Thus, to assess the influence of the increasing ambiguity of the edges as

the Gaussian blobs increased in size, the slope of the relationship between actual size and

estimated size was calculated for both stimulus classes within each participant.

The slope of the motor-implied estimates was not expected to be on the same scale as the perceptual estimates therefore direct comparisons across task type was not possible. Instead stimulus class within an estimation type was compared, and the relative inter-class patterns of the relationship was expected to yield insight into differential processing. Before the slopes were compared, linear R^2 fits of the plots were calculated to ensure the slopes represented the data appropriately. The R^2 of both stimulus types was greater than .98 and .63 for the perceptual and movement estimates, respectively. The large R^2 values indicated that the estimated size-actual size relationships fit the data well. The mean slopes for the perceptual estimates were 1.25 estimated-size/actual-size (SD = 0.15) for circles and 0.75 estimated-size/actual-size (SD = .14) for Gaussian stimuli. The slopes of the movement-based estimates were 0.06 (SD = 0.08) for circles, and 0.04 (SD = 0.07) for Gaussian stimuli. The perceptual estimates of width differed significantly in their slopes, $t(11) = 14.25$, $p < .01$. Comparatively, movement implied estimates of width did not differ significantly in their slopes between classes of stimuli, $t(11) < 1$, $p > .05$. As movements remained unbiased by the introduction of the ambiguous edges through the Gaussian blob stimuli, the movement system successfully and consistently interpreted the locations of the edge and thus appeared unbiased by modulations in the ambiguity of the edges of the stimuli. Therefore perceptual judgements of size became increasingly biased as the ambiguity of the edge increased. Movement-implied estimates of width on the other hand became less influenced by coupled increases of size and blur. This dissociation in the pattern of results between perceptual and motor-implied measures suggests that despite having common origins in early visual areas, each visual pathway is capable of generating different solutions regarding the location of a visual edge.

27
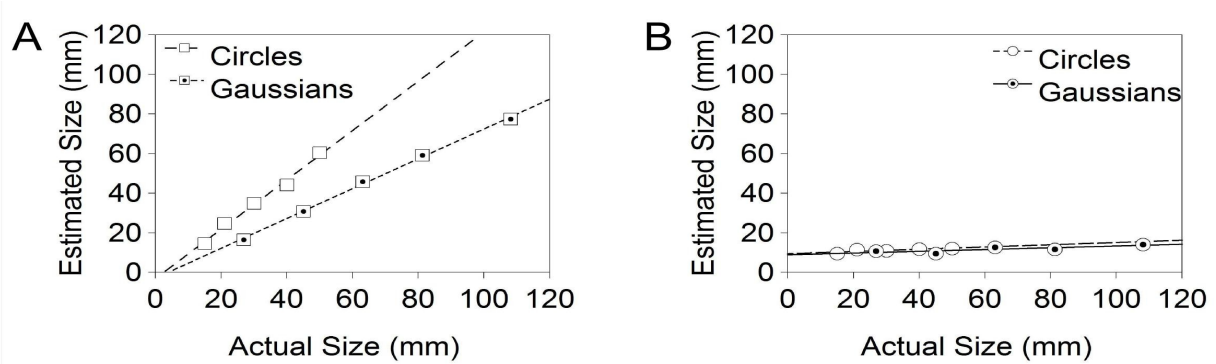
Figure 2.3: The rate of scaling of responses to changes in size in Experiment 1. (A) Perceptually estimated stimulus width plotted against actual width. Scaling to circle stimuli exhibited a greater slope than Gaussian stimuli. (B) Movement implied width plotted against actual size of stimuli. The slope of the relationship was no different between stimulus classes.

In the present investigation, the consistent underestimation of perceptual judgements of the location of the edges of the Gaussian stimuli was not a surprising outcome. Classical models of edge-detection such as that by Marr and Hildreth (1980) posit that the perceived location of an edge should occur at the zero-crossings of the second derivative of the luminance profile. If the second derivative were used to determine edge location perceptually, a steeper slope of luminance decay would yield less biased estimates of the edge location. That is, the location of the second derivative of the decay would indeed be located closer to the true edge. Moreover, curved edges were used and previous research showed that this may also have accentuated any inward bias in the localization of the edges (Mendonca, Padfield, Miller, & Turek, 2004). Specifically, simulation findings suggested that if the location of a curved edge is determined

through a second derivative model via gradient descent (down the edge), then gradually varying

edges result in an inward bias in the localization of curved edges (Mendonca et al., 2004).

Importantly however, if both the perceptual and motor systems relied upon the same second-

derivative model for the localization of edges, then one would have expected similar biases

towards the Gaussian stimuli relative to the circles. This was not the case. The perceptual system

was significantly biased by the blurred stimuli whereas the motor system was not. Therefore the

two visual streams appear to generate or at least utilize different spatial representations of edge

location.

2.3.4 *Conclusions*

The current findings challenge the notion that the localization of luminance edges is

completed prior the bifurcation of the ventral and dorsal visual streams. Specifically, if

information were common to both pathways then the prediction is for equivalent edge

localization between systems regardless of edge blur. The present investigation showed that the

ventral and dorsal streams may not in fact be passive recipients of edge information from lower

visual areas and may actually independently construct their own estimates from the information

passed to them. Thus a model of human visual processing which permitted the possibility of

unique representations such as either the Perception-Action model (Milner & Goodale, 1995) or

the Planning and Control model (Glover, 2004) was supported over models which did not permit

the existence of unique representations (e.g., as the Unitary Representation perspective of Franz

et al., 2000). Although edge blur has been proposed to be the primary factor influencing the

biases in the perceptual system, the findings do not rule out a possible influence of object size

either acting alone or interacting with edge blur. Further investigations will attempt to identify the

influences of blur and size in a fully factorial manner.

2.4 *Experiment 2: Perception and Prehension towards Blurred Stimuli*

2.4.1 *Introduction*

Experiment 1 hypothesized that the processing of luminance edges in early visual areas would result in equivalent ventral and dorsal estimates of edge location. This prediction was based upon previous research involving an alignment task (Gegenfurtner & Franz, 2007) and an orientation-based visual illusion (Dyde, & Milner, 2002). Task difficulty was increased to elicit luminance-driven performance degradation by presenting 2D Gaussian luminance blobs with varying levels of edge blur. The findings of Experiment 1 were that as edge blur increased perceptual judgements became increasingly biased and underestimated edge location. Motor responses scaled equally to alterations in size regardless of edge blur. The implication of these findings was that edge location information was not simply passed to both visual streams from early visual areas, but that locations were independently constructed at higher visual areas within the ventral and dorsal streams despite their having arisen from common early visual centres.

In the previous investigation, edge-blur was systematically linked to the size of the Gaussian blob. This coupling was due to the fact that the peak contrast of all blob images was held constant, and resulted in the same absolute decay in intensity over a greater spatial extent as the SD, and subsequently the size of the blob increased. Therefore, it is premature to conclude that the blur of the edge alone is driving the effect. Experiment 2 was designed to address this issue by independently and systematically varying the size of the object and the blur of the edge. This was accomplished using modified Gaussian-like stimuli of known size and blur. Based on the findings of Experiment 1, the location of the blurred edge was expected to be available to both visual streams but differentially represented in each. Further, of the two processing streams,

increasing the level of blur was expected to have a greater influence on the perceptual (ventral) outcomes than the motor (dorsal) outcomes.

A conventional manipulation in the dual visual stream literature, the inclusion of a NVS condition (inclusion of a 2-seconds of delay) have been utilized to elucidate task-related differences in Experiment 2 (Section 2.4). The importance of a delay comes from studies favouring unique representations (e.g., Hu & Goodale, 2000, Ganel, et al., 2008). Particularly strong evidence comes from the double-dissociation between visual-form-agnosics and optic ataxics in FVS versus visual-delay conditions (Milner & Goodale, 1995, Milner Paulignan, Dijkerman,,Michel, & Jeannerod, 1999). Although visual-form-agnosics have difficulty identifying visual stimuli, they can accurately interact successfully with them under FVS, but under NVS conditions their performance deteriorates (Milner & Goodale, 1995). Conversely, although optic ataxics do not have difficulty identifying visual stimuli, they can accurately interact successfully with them under NVS but not FVS conditions (Milner et al., 1999). These findings are taken as evidence that visual-form-agnosics experience deficits in their perceptual representation (Hu & Goodale, 2000) whereas optic ataxics experience deficits in their motor representation.

To test the notion that the two visual streams utilize unique representations of edge location, a pilot experiment was performed assessing the influence of the direction of contrast of stimuli on perceptual and motor-based outcomes (see Appendix A). Preliminary findings revealed no differences, and the manipulation as was abandoned (see Figure A.1). Subsequently a 2-s visual delay (removal of stimulus from view) was instead introduced to create a NVS response condition. Specifically, the ventral steam has been shown to retain relatively high-resolution information for longer durations (i.e., > 2 sec) prior to the queueing of a response. Conversely,

the dorsal stream representation is generally considered instantaneous, and thus should demonstrate poor NVS performance. Thus, if a single unitary representation were to guide both perceptual and motor-implied estimates following a delay, comparable decay of the representation should be expected to be evident in both. If on the other hand unique representations guided the perceptual and motor-implied responses, differential decay would be possible.

2.4.2 *Materials and Methods*

    2.4.2.1 *Participants.*

    Thirteen university aged individuals (6 male, 7 female, mean age $M = 25.15$ years) were recruited for the study. All participants were right handed (by self-report) and had normal or corrected-to-normal vision. Informed written consent was given by all participants prior to commencement of the experiment.

    2.4.2.2 *Apparatus.*

    The custom apparatus used for stimulus presentation and data collection purposes was modelled in a similar fashion to the apparatus used by Krigolson and Heath (2006, but see Held & Gottlieb, 1958 for an earlier incarnation). The main surface for the experimental tasks was a table-top measuring 120 cm wide by 60 cm deep. A second, parallel surface was positioned 35cm above this surface. This second-level surface consisted of a two-way mirror with the reflective surface facing away from the table-top (i.e., towards the ceiling). A third surface was positioned 35 cm above the mirror surface. A downward-facing LCD monitor screen (25" Dell 3007 WFPHC wide-screen) was mounted in the top surface. Images presented on the screen appeared on the surface of the mirror when the mirrored was viewed from above. As the distance between the monitor's screen and the mirror was matched with the distance of the mirror to the tabletop,

images projected from the monitor appeared to be presented upon the tabletop rather than on the mirror. Both the table-top and the mirrored surface were angled approximately 6.5^{O} towards the participant. When seated in front of the apparatus with the head in a chin-rest above the mirrored surface, stimuli displaced on the monitor screen appeared to be in located the same plane (i.e., on the tabletop surface) as their hands. Light-emitting-diodes (LEDs) were secured to the tips of the right thumb and index finger as well as the radial surface of the wrist of the right hand as the mirrored surface prevented participants from directly viewing their hands. Thus, when the LEDs were illuminated, the location of the wrist and fingertips in space was revealed to the participants. IREDs were also placed upon the tips of the right index finger and thumb. A third IRED was placed on the thumb-side of the metacarpal-phalangeal joint of the right index finger. The fingertip/thumb-tip IREDs were used to monitor the degree of opening of the hand during grasping (grip aperture), while the third IRED tracked the movements of the hand through space.

2.4.2.3 *Stimuli.*

Each stimulus was generated as a 1280 by 768 pixel image. Three sizes of stimuli were generated with four levels of blurring. The stimuli were initially all uniformly black circles of unique widths overlaid upon a grey background. A 2D zero-lag Gaussian filter was then passed over the image resulting in blurred edges. The width of the Gaussian filter determined the degree of blurring of the edge. Peak contrast was equated for all stimuli following the filtering process by rescaling the image to include the same range of luminance values. The four levels of blur were named through the relative rates of change (slope) in luminance over space induced by the filter. They were shallow (longest blur), medium (intermediate blur), steep (shortest blur) and infinite (no blur). Stimuli with infinite slopes were not filtered and remained as uniform solid circles. The blurs subtended 1.5, 1.0, 0.5, and 0 cm, representing shallow, medium, steep and

infinite slopes, respectively. Three sizes of stimuli were displayed upon the screen with diameters

of 5 cm (small), 6 cm (medium) and 7 cm (large) across. Stimuli with equivalent size but

different levels of blur were generated by manipulating the diameter of the circle to-be-filtered.

Therefore, a total of 12 stimuli images were created and organized as three sizes (i.e., small,
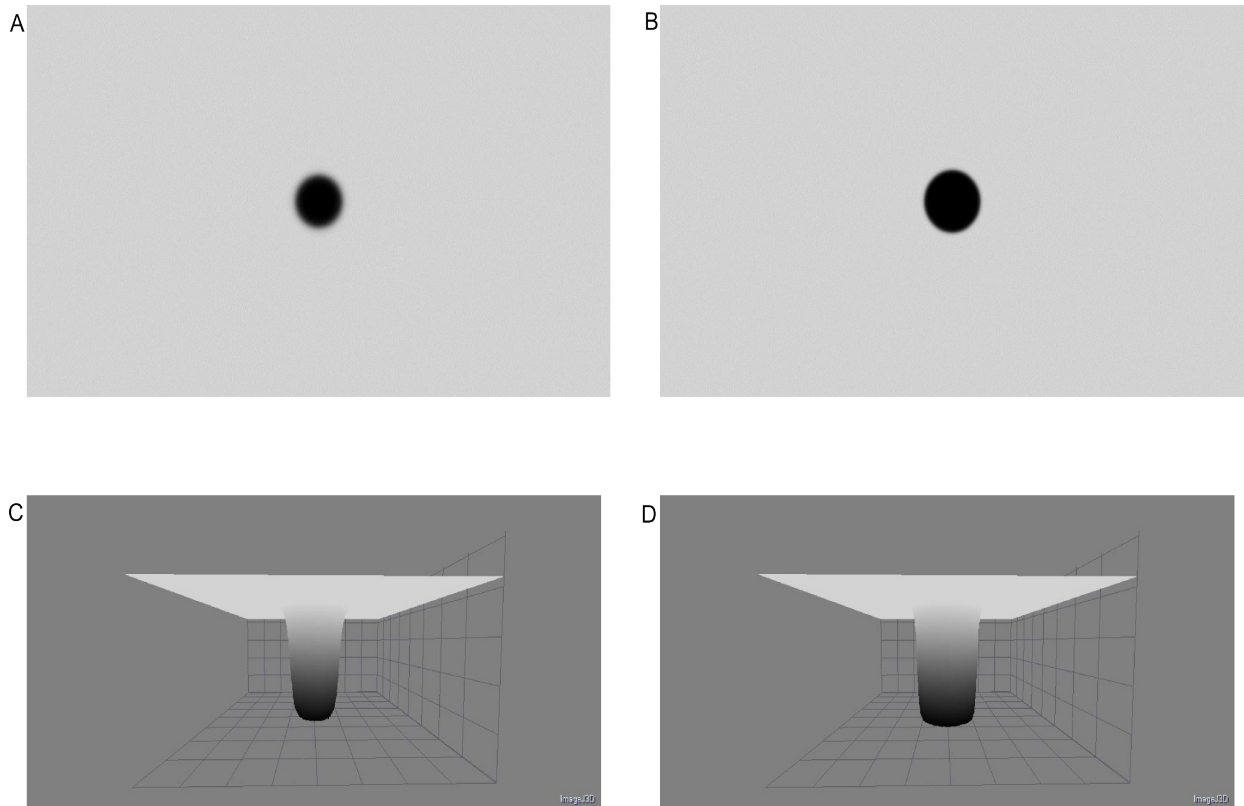

Figure 2.4: Two example stimuli from Experiment 2. (A) medium blur; (B) steep blur,3D

representations of luminance profile (C and D). (C) 3D representation of luminance profile of

medium blur. (D) 3D representation of luminance profile of steep blur.

medium, large) and four levels of blur (i.e., shallow, medium, steep, infinite) (See Figure 2.4 for examples). Three plastic cylinders, which were matched in width to the three sizes of stimuli were placed below a stimulus image of corresponding size to provide accurate haptic feedback to participants.

2.4.2.4 *Procedures*.

Each participant completed 4 blocks of 72 trials, and each block contained 6 trials of each of the 12 unique stimuli. Two blocks were completed under FVS and two were completed under NVS conditions (following a 2-s delay with no vision of the hand or stimulus). Within each visual condition, one block consisted of perceptual-estimation trials, and the other consisted of grasping trials. The order of the 4 blocks was independently randomized for each participant at the start of their experiment. In all conditions, participants sat in front of the apparatus with their chin situated on a chin-rest above the mirrored surface. Participants wore liquid crystal vision occluding goggles (LCD Goggles, Milgram Technologies) which afforded the experimenter the ability to manipulate the availability of vision of the experimental setup to the participant. Within the FVS condition blocks, both the stimulus and the participants' hand were visible for 4 seconds prior to the go-signal (i.e., 2-s preview then 2-s FVS delay). Vision of the stimulus and the participants hand persisted for the remainder of the trial. In the NVS blocks, both the stimulus and the participants' hand were initially visible for 2 s and removed for an additional 2 s prior to the go-signal (i.e., 2-s preview then 2-s no-vision delay), with the stimulus and hand remaining hidden for the remainder of the trial.

The task in the perceptual-estimation trials was to match the size of a comparison-circle on the right half of the display, to the size of a stimulus presented on the left half of the display. The "up" and "down" arrow-keys on a keyboard were used to adjust the size of the comparison

circle on the right half of the screen. When satisfied with the size of the comparison circle, the

enter key was pressed to save the estimate (See Figure 2.5). The appearance of the comparison-

circle upon the right side of the screen was the cue to begin estimating the size of the stimulus.

The starting size of the comparison circle for half of the trials to a given stimulus (3 trials) was 1

pixel (approximately 5cm smaller than the small stimulus size). In the remaining trials, to a given

stimulus the starting size of the comparison circle was 240 pixels (approximately 5 cm larger than
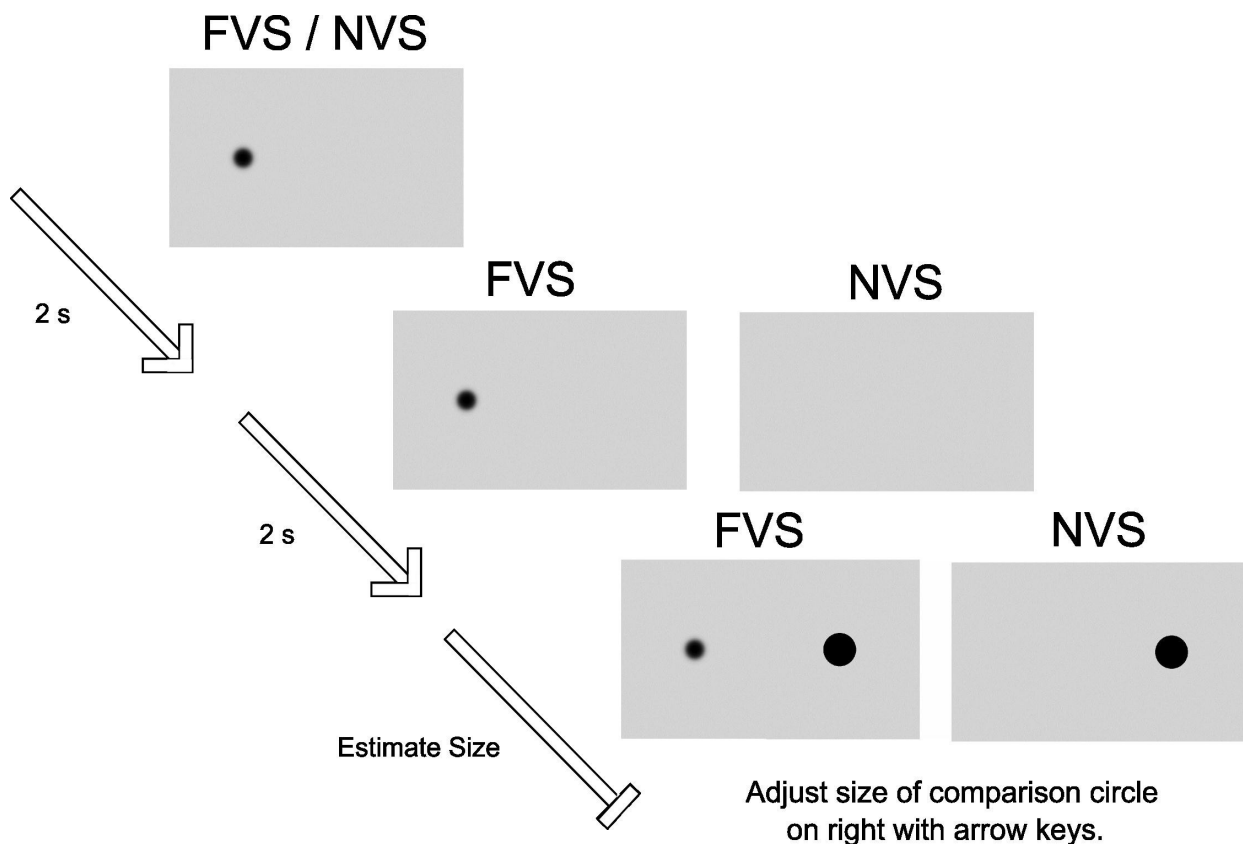

Figure 2.5: Trial progression of Experiment 2 perceptual-estimation trials. In the FVS condition

vision of the target and hand were available. NVS represents the condition where vision of the

target and hand were extinguished for two seconds prior to the initiation of the response.

the large stimulus size). This manipulation was performed to avoid any directional biases in the

estimations caused by size-contrast effects (see Aglioti et al., 1995 for an example).

The task in the grasping trials was to reach-for, grasp, and lift a stimulus at the sound of an auditory go-signal (See Figure 2.6).When participants grasped a stimulus (an image), they actually grasped the corresponding cylinder which was superimposed below the stimulus. Prior to the start of a grasping trial, participants placed their right hand the "home" position represented by a notch on the tabletop. The LCD goggles were then closed, and participants had no view of the experimental setup. This allowed an experimental confederate to know the upcoming stimulus size and to place the plastic cylinder of corresponding size upon the tabletop. Participants then verbally declared their readiness and the experimenter initiated the trial. The LCD goggles opened, the participant saw a fixation cross in the middle of the screen which remained present for 1 to 2 s, and the LEDs were illuminated. The stimulus was then displayed for a preview period of 2 s. Following the preview period, the stimulus persisted for an additional 2-s window prior to an auditory go signal. In the NVS condition, following the 2-s preview the stimulus disappeared and the LEDs were extinguished (removing visibility of both the stimulus and the hand) for 2 s prior to the go-signal. When participants reached out to grasp the displayed stimulus they physically interacted with the corresponding cylinder which was superimposed with the stimulus. Following the completion of the grasping trial, the participant returned their hand to the home position, the goggles were closed, and. the subsequent trial was then revealed to the experimental confederate.

2.4.2.5 *Design and Analysis.*

As in Experiment 1, confirmatory analysis was performed on the movement-related data to ensure the movement patterns in the grasping task were comparable to similar grasping
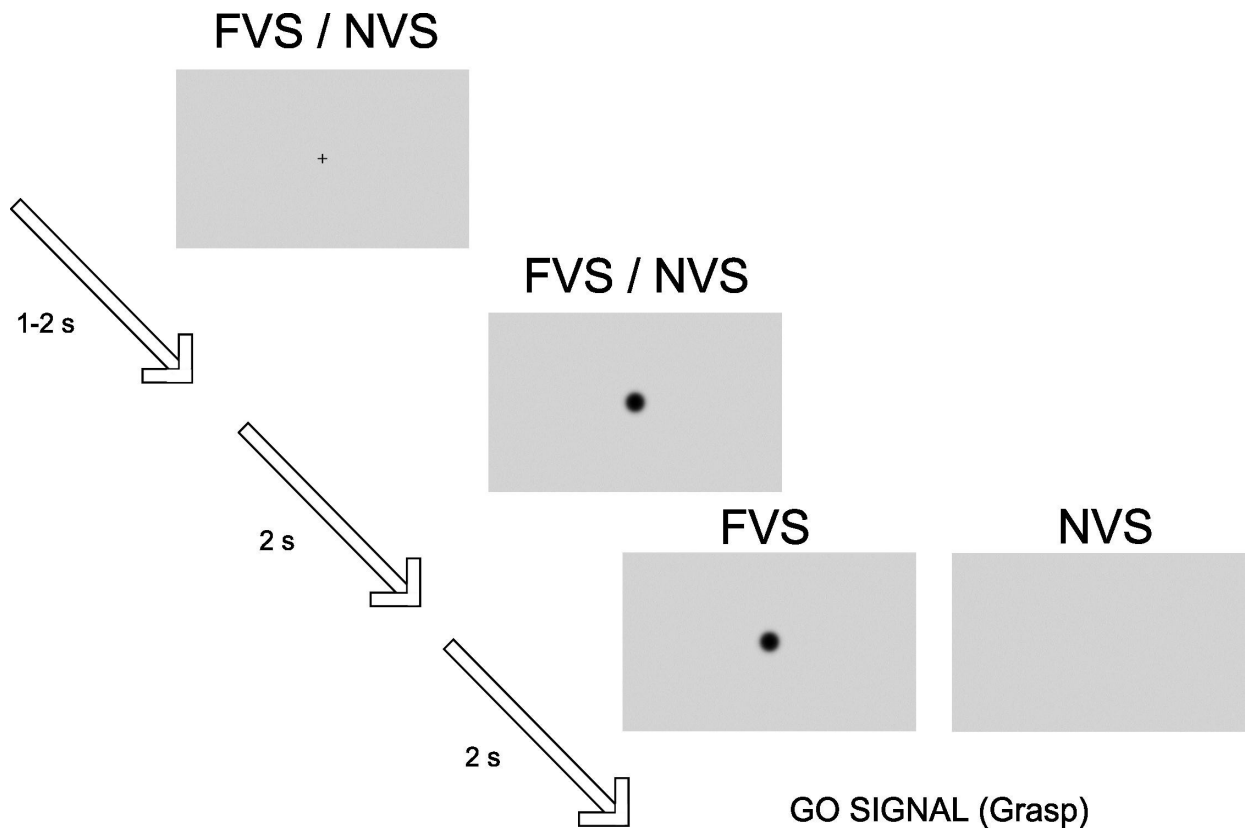
Figure 2.6: Trial progression of Experiment 2 grasping trials.

movements described in the literature. These included RT, MT, maximum-maximum grip aperture (MGA), and percent MT of maximum grip aperture (PtMGA). An additional kinematic analysis, the dynamic illusion effects analysis was performed to assess the influence of blur upon grip-aperture across the duration of the movement. If the omnibus ANOVAs indicated significant statistical differences between levels, then post-hoc tests were conducted with a Bonferroni-corrected simple main effects approach. Subsequent to the confirmatory analysis within each task and for each of the 4 levels of blur, the slope of the rate of scaling of estimates across the 3

stimulus sizes were calculated, resulting in 8 slopes per participant. These slopes were calculated to ascertain a direct comparison with the previous literature. Experiment 1 demonstrated that, even under non-biasing conditions, the scaling of motor and perceptual responses to changes in size could be expected to differ. The slopes of the non-blurred stimuli were then used to transform the slopes of the blurred stimuli into a common metric that could be compared across tasks. This normalization procedure was computed within each task by dividing the slopes of each level of blur by the slope of the infinite stimuli. A 2 (task: perceptual estimation, grasp) by 2 (visual-condition: FVS, NVS) by 3 (blur: shallow, medium, steep) repeated measures Analysis of Variance (ANOVA*)* was performed on the normalized slopes. A second slope analysis was performed to assess the direct influence of the level of blurring of the edges of the stimuli on estimates of target width. These blur slopes were quantified for each size of stimuli by plotting the estimated size by the number of mm of blur of the edge across levels of increasing blur. Thus a total of 6 blur slopes were generated for each participant (3 for perceptual estimates, and 3 for MGA). The blur slopes were analyzed in a 2 (task: perceptual estimate, grasp) by 2 (visual-condition: FVS, NVS) by 3 (size: small, medium, large) repeated measures ANOVA. If a different pattern of slopes (scaling) occurred across the two-tasks, especially across visual-conditions, the notion that the two visual systems utilize independent spatial representations would be supported.

2.4.3 *Results and Discussion*

     2.4.3.1 *Confirmatory Analysis.*

An initial examination of the data describing only the stimuli with the sharpest of edges was conducted to ensure that instructions were followed and task performance was comparable to classical stimuli (e.g., Aglioti et al., 1995). Thus, for grasping trials to infinite edge targets, RT,

MT, MGA and PtMGA were each assessed by a 2 (visual condition: FVS, NVS) by 3 (size: small, medium, large) repeated measures ANOVA. The three time-related relevant variables (RT, MT, and PtMGA) were chosen for this task because the timing of normal grasping movements has been well studied (see Jeannerod, 1984). The grand mean RT in the FVS condition was within the expected values for stimuli of comparable size ($M = 323.8$ ms (SD = 58.2) (Hesse, De Grave, Franz, Brenner, & Smeets, 2008). Similarly, the grand mean value for MT for a movement of 30 cm was 709.59 ms (SD = 120.21) which was also similar to previous findings (Paulignan, Mackenzie, Martenuik, & Jeannerod, 1991; Servos, Goodale, & Jakobson, 1992). The ANOVA on the RT yielded no significant main effects or interactions (all F's < .19, all p > .82, all partial η^2 < .02). MT showed a main effect of size ($F(2,24) = 4.53$, $p < .05$, partial $\eta^2 = .26$) (see Figure 2.7) which was indicative of MT to target size scaling (Fitts, 1954). No other main effects or interactions were present for MT (all F's < 2.34, all p > .12, all partial η^2 < .16).

The ANOVA performed on PtMGA revealed no significant main effects or interactions (all F's < .67, all p > .52, all partial η^2 < .05) indicating consistent relative time scaling during grasp. MGA was significantly influenced by changes in stimulus size, as evidenced by a significant main effect of size, $F(2,11) = 12.90$, $p < .01$, partial $\eta^2 = .70$ (Figure 2.7). Pairwise post-hoc comparisons revealed larger apertures to larger stimuli and significant differences between all levels of size (all $t's > 3.19$, all $p's < .05$).The main effect of visual-condition also neared significance ($F(1,12) = 4.62$, $p = .053$, partial $\eta^2 = .28$.) with NVS conditions resulting in larger MGA, a pattern expected from previous research (Hu & Goodale, 2000). As the patterns of the grasping data were well within expected values (Jeannerod, 1984), these data were taken as
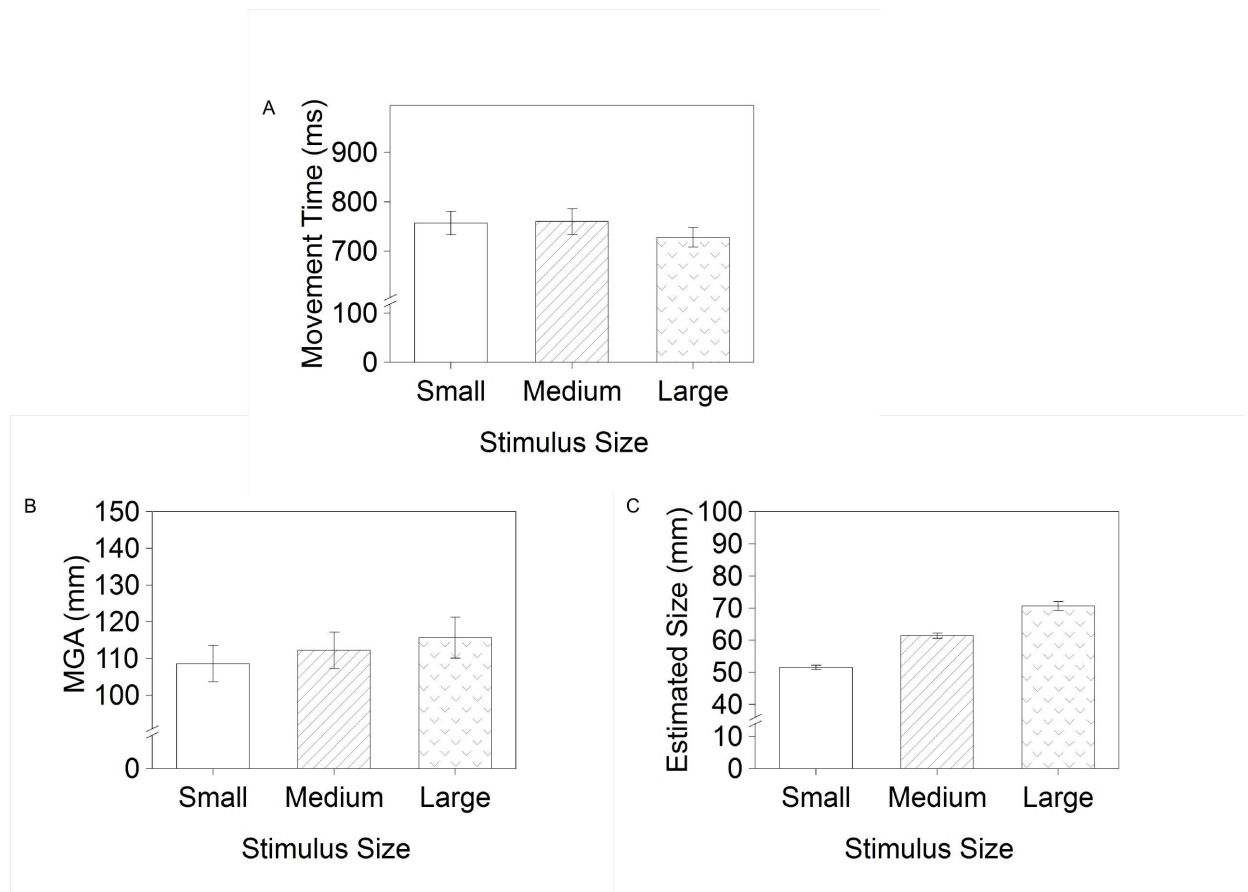
Figure 2.7: Confirmatory analysis in Experiment 2. (A) MT analysis of infinite edge stimuli showing MT to the largest stimuli were completed in a shorter amount of time than the smallest stimuli. (B) MGA analysis of non-blurred stimuli. MGA increased with increasing stimulus size.. (C) Perceptual-estimates of size. Estimates increased with increases in stimulus size. Error bars represent +/- 2 SEM.

 evidence that instructions were followed and the experimental grasping set-up was not biasing participants in an unusual way. In the interest of consistency, size approximations were also examined across visual-conditions and size for the perceptual-matching task as well. Perceptual

estimates of the size of infinite edge stimuli were influenced by the actual size of the stimuli, butnot the visual-condition ($F(2,11) = 194.70$, $p < .001$, partial $\eta^2 = .70$ (Figure 2.7) and $F(1,12) = 1.49$, $p = .246$, partial $\eta^2 = .11$, respectively), and post-hoc analysis revealed that all sizes were significantly different (all $t's > 10.05$, all $p's < .01$). Combined, the results of both the grasping and perceptual tasks suggest that participants were following the instructions of the tasks and were behaving in a manner consistent with both historical and current findings for grasping/perceptual tasks.

Confirmatory analysis was also run on the raw perceptual estimates and MGA data within task in a 2 (visual condition: FVS, NVS) by 3 (Size: small, medium, large) by 4 (blur: shallow, medium, steep, infinite) repeated measures ANOVA. The main effects of visual condition, size, and blur were assessed for each task. The analysis of perceptual estimates revealed main effects of size and blur, but not visual condition ($F(2,24) = 432$, $p < .01$, partial $\eta^2 = .97$; $F(3,36) = 447.65$, $p < .01$, partial $\eta^2 = .974$, and $F(1,12) = 0.25$, $p = .62$, partial $\eta^2 = .02$ respectively). Follow up post-hoc tests on size revealed differences between all sizes (all $t`s > 12.99$, all $p's < .01$). Post-hoc tests on levels of blur indicated that all levels were statistically different (all $t`s > 511.46$, all $p's < .01$). Regarding MGA, a main effect of visual condition was present ($F(1,12) = 12.36$, $p < .01$, partial $\eta^2 = .51$). MGA also exhibited a main effect of stimulus size ($F(2,24) = 51.79$, $p < .01$, partial $\eta^2 = .81$). Pairwise post-hoc comparisons revealed larger MGA to larger stimuli (all $t`s > 5.65$, all $p's < .01$). The main effect of blur was significant for MGA ($F(3,36) = 63.25$, $p < .01$, partial $\eta^2 = .84$). Post-hoc comparisons revealed differences between all levels of blur (all $t`s > 4.01$, all $p's < .05$) Both perceptual estimates and MGA scaled with increasing estimates to increases in stimulus size, and decreasing estimates to increases in blur. Only MGA was influenced by visual condition.

2.4.3.2 *Slopes Analysis.*

The rate of scaling (slope) of MGA to changes in stimulus size under FVS conditions was found to be 0.42 across all stimuli. While this value was smaller than the average value of 0.82 obtained in a review of the grasping literature by Smeets and Brenner (1999), it fell close to a recently reported value of 0.5 (Franz, Hesse & Kollath, 2009). Perceptual scaling was much closer to unity as the average rate of scaling to changes in size was .89. As the raw rates of scaling of the two tasks were expected to be different (see Smeets & Brenner, 1999), the direct analysis of size-estimates between the two tasks was not directly interpreted. Specifically, because MGA is an implied estimate rather than directly the outcome of a movement, estimates of size achieved from measuring MGA are often closely related to stimulus size, but tend to overestimate it (Smeets & Brenner, 1999). Also interestingly, the scaling of perceptual estimates was closer to the expected rate of MGA scaling. This finding was judged to be coincidental as the rates of scaling of both tasks were reduced in the presence of edge ambiguity. Thus the simple comparison of size estimates or size slopes may not be a strong enough argument to conclude the existence of unique feature representations between the two visual streams (ventral and dorsal).

The normalized slopes analysis of a 2 (task: perceptual estimate, grasp) by 2 (visual-condition: FVS, NVS) by 3 (blur: shallow, medium, steep) repeated measures ANOVA yielded a significant main effect of visual-condition ($F(1,12) = 4.8$, $p < .05$, partial $\eta^2 = .29$), and a task by visual-condition interaction ($F(1,12) = 7.4$, $p < .05$, partial $\eta^2 = .38$). The main effect of task was not significant ($F(1,12) = 0.138$, $p = .72$, partial $\eta^2 = .01$). A simple main effects analysis revealed that both the main effect and the interaction were driven by MGA under FVS conditions scaling with a steeper slope than MGA under NVS conditions ($t(12) = 2.6$, $p < .05$). The scaling of the perceptual estimates did not vary as a function of visual condition ($t(12) = .216$, $p = .8$) The

unique representation-based models of both Perception-Action and Planning and Control allowed for the possibility for differential slopes across tasks and visual conditions (See Figure 2.8). The Unitary Representation perspective of Franz et al. (2000) however, predicted that because both
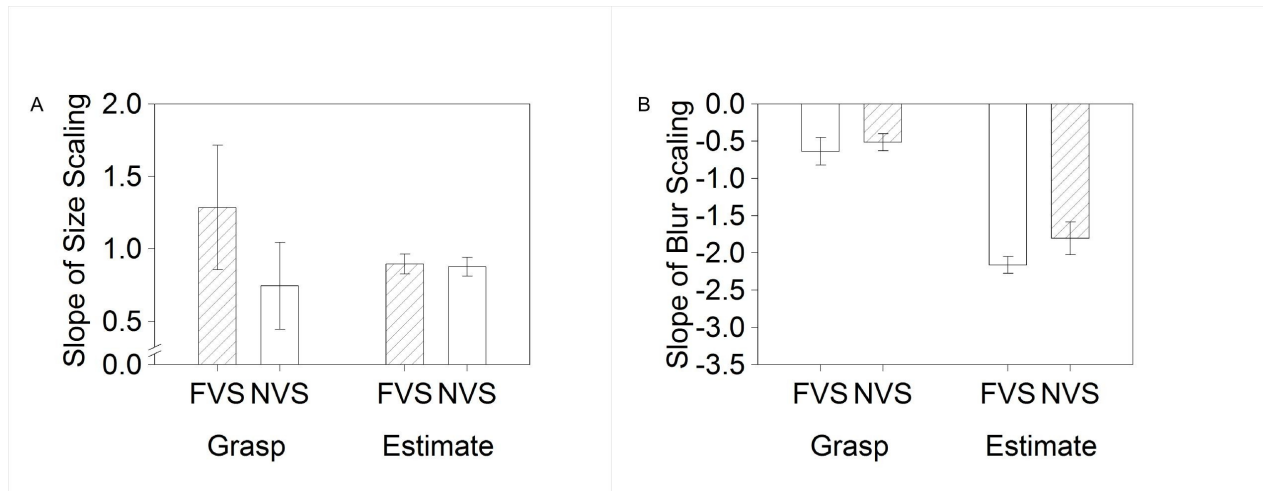
Figure 2.8: Slopes analysis of Experiment 2. (A) Normalized estimated-size/veridical size slopes in Experiment 2. A task by visual-condition interaction revealed that scaling of MGA was greater under FVS conditions, but converged with perceptual rates of scaling under delayed visual-conditions. (B) Estimated-size/degree-of-blurring slopes. A task by visual-condition Interaction Revealed that perceptual scaling became more shallow following a delay,. Error bars represent +/- 2 SEM

tasks utilized the same representation of object features, the scaling of both tasks should have been equivalent regardless of visual-condition. As the latter was not the case, the unique representation models were supported by the normalized slopes analysis.

The 2 (task: perceptual estimate, grasp) by 2 (visual condition: FVS, NVS) by 3 (size: small, medium, large) repeated measures ANOVA for the blur slopes resulted in main effects of task ($F(1,12) = 215.54$, $p < .01$, partial $\eta^2 = .95$) and visual condition ($F(1,12) = 8.47$, $p < .05$, partial $\eta^2 = .41$). The slope of the perceptual task was steeper than that for the grasping task, and the FVS condition yielded a steeper slope than the NVS condition. No significant main effect of size was discovered ($F(2,24) = 0.07$, $p = .93$, partial $\eta^2 = .01$). There was also a significant interaction between task and visual-condition ($F(2,11) = 6.18$, $p < .05$, partial $\eta^2 = .34$). The interaction was further analyzed using simple main effects and a significant difference was discovered between the two levels of visual condition within the perceptual-estimation task with FVS condition exhibiting a steeper slope than the NVS condition ($t(12) = -3.6$, $p < .01$). No comparable significant difference was discovered between visual conditions across the blur slopes for the grasping task ($t(12) = -1.34$, $p > .05$). The pattern of slopes revealed by the task by visual condition interaction for the blur slopes replicated the pattern of findings in Experiment 1. The perceptual estimation task was differentially influenced be increasing blur across visual condition whereas the grasping task was invariant to it. The fact that the perceptual task became less biased by the blur in a NVS condition was unexpected since perceptual estimations have been generally believed to be relatively persistent over time relative to motor-based estimates (Bradshaw & Watt, 2002; Hu & Goodale, 2000). One possible explanation for the decreased influence of blur in the NVS condition for perceptual estimates could be the adoption of a conservative strategy where the various levels of slope are treated with an equal but large degree of caution. Changes in motor responses such as increases in MGA in a NVS have been described as an adoption of a similar strategy (Hu & Goodale, 2000).

Research examining the influence of visual illusions has previously found that perceptual estimates under NVS conditions are generally consistent with their FVS counterpart conditions (Bridgeman & Peery, 1997). Only one experiment has attempted to systematically manipulate the length of delay in a NVS condition to even non-biasing stimuli (Bradshaw & Watt, 2002). It was found that perceptual estimates are uninfluenced by delays ranging from 0 s to 4 s. Pointing movements were found to suffer decrements in performance in as little as 2 s. Increases in uncertainty regarding visual-condition and target location have been found to result in the adoption of a conservative (worst-case-scenario) strategy for pointing movements (Hansen, Glazebrook, Anson, Weeks & Elliott, 2006). The decrease in the rate of scaling of estimates of size to blurred edges in the NVS condition of the current experiment could be similarly explained by the adoption of a highly conservative strategy. If the completion of a NVS response to blurred stimuli resulted in sufficient uncertainty about the edge location, then the visual output systems (perceptual/motor) may have performed in a more similar manner to all levels of blur in an attempt to perform adequately in a worst-case-scenario situation. The notion of the utilization of a conservative strategy performed in a good-enough way to accomplish the goal has been defined as satisficing the task (Simon, 1955). Satisficing has been successfully applied to the modelling of pointing and grasping movements by simply applying a number of constraints to the movement rather than attempting to optimize performance (Rosenbaum, Loukopolous, Meulenbroek, Vaughan, & Engelbrecht, 1995; Rosenbaum, Meulenbroek, Vaughan, & Jansen, 2001). The major constraint requiring satisficing within the grasping task in the current investigation could be described as ensuring the grip-aperture exceeded the width of the stimulus during the reach. If the spatial extent of the stimuli became increasingly uncertain in a NVS condition, then treating all blurred stimuli equally cautiously could be a good-enough,

conservative strategy to complete the task. Also an increased scaling to changes in size of blurred stimuli in FVS could be interpreted as an adoption of a satisficing strategy by performing increasingly more conservatively (greater MGA) to increases in size. The successful completion of the perceptual task was not similarly constrained by physical means, as an underestimation would not result in a failure to complete the task. The increased uncertainty about the edge location in the NVS condition did however, result in smaller influences differences in the reported sizes of the blurred stimuli. Thus the adoption of a more conservative (satisficing) strategy for perceptual estimates in the NVS condition existed such that participants did not adjust their estimates inward in a NVS condition compared to the FVS. This pattern coupled with the adoption of a conservative (satisficing) strategy in size scaling in the FVS condition compared to the NVS for the motor-based task supported the notion of unique representations between the visual streams because of a differential pattern of strategies was employed across visual condition and task..

The pattern of results provided support to the unique representation models of Perception-Action and Planning and Control as compared to the unitary representation model The rate of scaling attained via the perceptual and motor-based tasks not only scaled differently to changes in size and to changes in edge blur, but also exhibited differential scaling in compared to perceptual estimates in a NVS action.

2.4.3.3 *Dynamic Illusion Effects Analysis.*

Although the presence of differential task scaling (i.e., normalized-rate) combined with task by visual-condition interactions for grasp supports the notion of a unique representation model over a unitary representation model, the data failed to distinguish between the competing unique representation models The major difference between the Perception-Action model and the

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Planning and Control model is the influence of the two visual streams upon the planning of movements. Under the Perception-Action model both the planning and control of movements are mediated by the dorsal stream of the visual system. The Planning and Control model on the other hand states that the planning of movements is heavily influenced by ventral functioning (perceptual representations). Visually guided hand movements have long been described as containing two phases: an initial ballistic phase, and a homing-in phase (Woodworth, 1899). In the ballistic phase the hand is thrust into the vicinity of goal of the goal of the movement, while the homing-in phase occurs when feedback is utilized to ensure an accurate movement. The ballistic phase of a movement is believed to be predominantly pre-planned, and therefore errors in planning could be expressed by differential measurable biases throughout the course of a movement. The Perception-Action model suggests that both phases of a movement are under the influence of dorsal stream processing, and therefore no dynamic influences of perceptually biasing stimulus features should be present. The Planning and Control model suggests that perceptual (ventral stream) processes influence movement planning and therefore the presence of perceptual biases should exert a dynamic influence on an ongoing movement. A dynamic illusion effects analysis was therefore conducted in order to differentiate the dualist models. A dynamic illusion effects analysis searches for a changing influence of an illusion across a movement (see Franz, 2003; Glover & Dixon, 2002). The effect was calculated using the difference between each blurred stimulus and the non-blurred stimulus of equivalent size at each movement decile (10^{th}s), and dividing that difference by the rate of scaling of grip-aperture (the distance between the tip of the index finger and thumb) to changes in size of the infinite edge stimuli at the decile. This approach was modelled after the one utilized by Franz (2003). Computationally an example of the calculation would appear as (infinite – blurred) / (rate of scaling of grip-aperture to changes in

size of infinite) at any specific decile of the movement. The deciles of movement chosen for the analysis were 30%, 40%, 50%, and 60%. Earlier deciles were not included in the analysis because variability at the earliest points in the movement is generally significantly larger (Glover & Dixon, 2002). Deciles later than 60% were removed as initial contact with the to-be-grasped stimulus can occur shortly after MGA and could artificially bias subsequent scaling (Franz 2003). Grip aperture was submitted to a 2 (visual condition: FVS, NVS) by 3 (Blur: shallow, medium, steep) by 4 (Decile: 30%, 40%, 50%, 60%) repeated measures ANOVA. The analysis revealed no statistically significant main effects or interactions, and thus any biases that were present in grip-aperture were non-differentiable across the movement. According to the Planning and Control model, perceptual biases should influence the early phases of a movement and result in a dynamic decrease in bias across the length of the movement. This dynamic reduction should occur only in the presence of vision. The Perception-Action model, on the other hand, predicts no evidence biases at any point during movement execution when vision is available for planning. The current investigation revealed no evidence for the presence of dynamic influences of stimulus features across the movement deciles examined. The finding of a consistent rather than a dynamic bias in grip aperture across the movement supported the Perception-Action model over the Planning and Control model.

2.4.4 *Conclusions*

Although visual luminance edge information is processed prior to the bifurcation into the ventral and dorsal streams of processing, the current investigation supports the notion that the visual streams generate unique representations of stimulus features. The clearest support for the presence of unique representations stemmed from the demonstration of task by visual-condition interactions for two different slopes approaches for MGA scaling (i.e., change in size and change

in edge blur). The normalized size interaction resulted from grasping estimates (MGA) scaling

uniquely under FVS conditions and converging with the normalized scaling of the perceptual

estimates under NVS conditions. The initial difference and subsequent convergence of values was

predicted by the unique representation models of Perception-Action (Milner & Goodale,1995)

and Planning and Control (Glover, 2004), but not unitary representation model (Franz et al.,

2000). To help differentiate the competing unique representation models, more detailed

movement characteristics were examined. The critical comparison which differentially supported

the Perception-Action model over the Planning and Control model was the absence of a dynamic

influence on the scaling of grip-aperture to the blurring of the edges across the movement. Thus

the ventral stream (through overt perceptual estimates) and the dorsal stream (through motor-

implied estimates) generated unique representations of specific stimulus feature information

(luminance edge locations) from which to guide their ultimate outcomes.

2.5 *General Discussion*

2.5.1 *Predominant Support for the Perception-Action Model*

Experiment 1, provided support for the unique representation based models of Perception-

Action (Milner & Goodale, 1995) and Planning and Control (Glover, 2004). That is that

perceptual estimates differentially scaled to stimuli with ambiguous edges, whereas pointing

movements scaled similarly irrespective of edge ambiguity. Experiment 1 provided evidence for

the possibility of unique representation of stimulus features, and Experiment 2 further examined

the relationships governing the visual interaction with stimuli with ambiguous edges. In

Experiment 1 the perceptual estimates were obtained by using a calliper to match stimulus width

whereas in Experiment 2 estimates were obtained by matching a test stimulus to a comparison

stimulus. Although both perceptual tasks were similar to those used in previous experiments (Hu

& Goodale; 2000, Franz, 2003), Experiment 2 allowed for stimulus judgement as a whole, rather than simply across a single dimension. The motor tasks in Experiment 1 and Experiment 2 were pointing movements and grasping movements respectively. Effective target width was the primary of pointing movements in Experiment 1 scaled with increases in veridical stimulus size, in accordance with previous work (Schmidt et al., 1979). A more well documented method for the acquisition of motor-implied estimates of size is the scaling of MGA (Aglioti et al., 1995; see Smeets & Brenner, 1999 for a review). The scaling of effective target width to increases in stimulus size are based upon the notion that as stimuli increase in size MT to those stimuli in pointing movements decreases (Fitts, 1954). Increases in MT have also been documented to be associated with increases in effective target width (Schmidt, et al., 1979). As a result, effective target width is expected in increase with increases in stimulus size. Unfortunately the indirect nature of this relationship makes the difficult to interpret. MGA on the other hand is a much more direct measure of movement implied size estimation. In Experiment 1 the stimuli were not factorially arranged across class in terms of size, and therefore direct comparisons of estimated stimulus sizes were not possible. This limitation was corrected in Experiment 2 with direct comparisons revealing scaling differences between sizes, degrees-of-blur, and tasks.

The critical comparison proposed to finally dissociate between the classes of models was demonstrated using a normalizing procedure to the rate of scaling of the tasks. Level of blur did not interact between the two tasks, demonstrating that both visual streams were biased by increasing blur. The finding that both visual systems were biased by changes in the quality of the edge was consistent with the findings of Dyde and Milner (2002), who reported that features which are processed early enough in the visual system should bias both visual streams. This work, however, did not predict the observed task by visual condition interactions. Specifically,

the pattern of the interaction (i.e., the convergence of motor scaling to perceptual rates following a delay) can be parsimoniously explained as a shift from the utilization of one stream's representation to another (Hu & Goodale, 2000). If unique representations exist between the two visual streams and the differences in the representations stemmed simply from their different goals, then there would be no reason to anticipate differences in feature representations which are processed prior to the bifurcation into two streams. If on the other hand, each processing stream generates its own representation based upon all the information available, regardless of the level when the information was first available, one could expect differential estimates of early processed stimulus features such as edges in the outcomes of the two visual streams.

The latter explanation was preferentially supported through the presence of a task by visual condition interaction. A shift from a unique scaling of motor-based responses towards the responses of perceptual estimates of the same stimuli under NVS conditions has been previously reported (Hu & Goodale, 2000). Without the inclusion of the NVS condition in Experiment 2, it would not have been possible to draw conclusions about whether the visual systems behaved in a manner consistent with the unique representations of stimulus features. The data could have been equally explained through either a unitary or a unique representation model. The existence of scaling differences, and especially task by visual-condition interactions, provided support for the possibility of unique representations of stimulus features within the dual streams of processing in the human visual system. Therefore the models of Perception-Action, and Planning and Control were preferentially supported over the unitary representation model.

Having established that a unique representation model better predicted the findings, a critical comparison was required to differentiate between the remaining competing models. Under many circumstances the Perception-Action and the Planning and Control models predict and are

supported by similar data. Both models expect and account for differences existing between motor and perceptual outcome variables. The difference between the two lies in the notion that under the Perception-Action model both the planning and the control of visually guided movements are governed by the non-conscious functioning of the dorsal stream, whereas the Planning and Control model allows for conscious perceptual experiences to influence movement planning, but not control. This position is founded on observations that the earlier phases of a movement were more heavily influenced by changes in movement planning and perceptual biases could be measured at early stages of a movement (Glover & Dixon, 2002). However, Franz (2003) subsequently found a lack of dynamic influences of illusions on MGA. The findings of the Glover and Dixon (2002) were explained as an artifact from the inclusion of very early and late portions of the movement being included in the analysis. The analysis of the current experiment were computed in a similar manner to Franz (2003) and ran counter to the Glover and Dixon (2002) findings in that there was no evidence of a dynamic influence of blur upon maximum-grip-aperture.

Thus, the current research supported the position that unique representations of stimulus edge features govern perception and action. A detailed evaluation resulted in the conclusion that the Perception-Action model (Milner & Goodale, 1995) was preferentially supported over both the Planning and Control model of Glover (2004) or the unitary representation model of Franz et al. (2000).

2.5.2 *Alternative Explanation: Feature Representations*

Although the current investigation preferentially supported the Perception-Action model of human vision over the other models considered, insights from a unique feature of the

experiments allowed for the reinterpretation of older findings and the expanding upon the supported model of human vision. The uniqueness of the current line of research stems from thefact that a large number of studies that have found a dissociation between perception and action in normal individuals have done so through the modification of the surroundings of a stimulus and not the stimulus itself (Aglioti et al., 1995; Binsted, Brownell, Vorontsova, Heath, & Saucier, 2007; Bridgeman, Gemmer, Forsman, & Huemer , 2000; Heath Neely, Yakimishyn, & Binsted , 2008; Hu & Goodale, 2000; Westwood & Goodale, 2003). Most of the studies relied upon context-based visual illusions or variants of illusions such as the Ebbinghaus illusion, the Muller-Lyer illusion or the induced-Roelofs effect (See Figure 2.9). Still other investigations utilized context-based masking paradigms (e.g., object-substitution-masking; for examples see Di Lollo, Enns, & Rensink, 2000; Binsted, Brownell, Vorontsova, Heath, & Saucier, 2007, Heath, Nealy, Yakimishyn, & Binsted, 2008) which significantly hindered perceptual report when motor responses remained accurate. A general consensus arising from these studies has been that the ventral stream works in relative metrics and is influenced by context-based illusions, whereas the dorsal stream remains largely invariant to context effects by working in absolute metrics and therefore effectively ignores task-irrelevant contextual stimuli. Each of the two visual streams have therefore been described as having its own unique stimulus representation with ventral representations in relative metrics and dorsal representations in absolute metrics.

The current investigation expanded upon the literature examining the two visual stream model of human vision by directly altering characteristics of the test stimulus itself rather than by manipulating the contextual surroundings of a stimulus. Generally, under unique representation models of human vision such as the Perception-Action model (Milner & Goodale, 1995) and the Planning and Control model (Glover, 2004) perceptual representations (ventral stream) can be
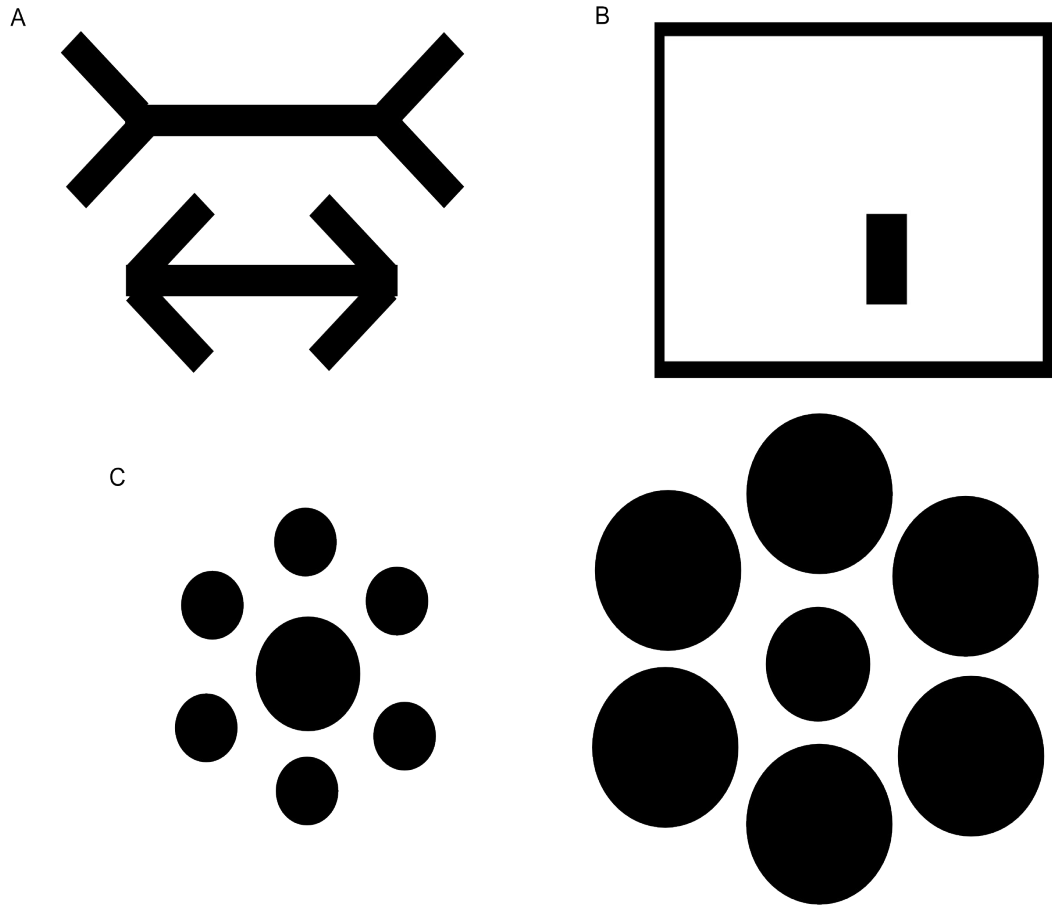
Figure 2.9: Commonly utilized context-based visual illusions. (A) The Muller-Lyer illusion. Context inducing fins result in the perception of longer lines in the fins-out orientation as compared to the fins-in orientation. (B) Induced Roelof's effect. The offset of the context-inducing frame around the object results in the perception that the object has been spatially shifted in the opposite direction. Especially under NVS conditions. (C) The Ebbinghaus Illusion/Ticherner Circles. Circles surrounded by larger circles appear smaller than those surrounded by smaller circles.

biased while the dorsal stream is believed to store an accurate representation of a stimulus (Aglioti et al., 1995). If the perceptual bias had been instantiated by visual processing prior to the bifurcation into the two visual streams, both streams would be predicted to suffer from the same biased information (Dyde & Milner, 2002). A lone example in the literature where similar stimulus properties were modified in an examination of the two visual streams of human vision was a study by Gegenfurtner and Franz (2007). They used 2D Gaussian blobs to compare location judgements of perceptual estimates to pointing movements. They found similar patterns of location estimation between tasks and concluded that motor and perceptual judgements of the ambiguous stimuli were represented by a unitary representation. While Gegenfurtner and Franz (2007) argued that a unitary representation model was best supported, unique representation based models could adequately explain the same data. As the modified stimulus feature was the edge, and edges are an early processed visual feature (Hubel & Wiesel, 1968), according to the Dyde and Milner (2002) account the edge information could have been passed on to and incorporated into unique representations governing both perception and action. Although Gaussian blob stimuli were utilized by Gegenfurtner and Franz (2007), the degree of ambiguity was not directly manipulated as all stimuli were of equal size and consequently of equal ambiguity. Instead the location of the blobs was systematically manipulated. The current set of experiments directly manipulated the intrinsic edge information of the Guassian-like stimuli and, therefore, was a better test of how early information is passed on to the two visual streams.

The choice in the utilization of 2D Gaussian stimuli and stimuli blurred with a 2D Gaussian distribution that were used in the current research was influenced by the equivocal support to studies looking for dissociations between perception and action using context-based visual illusions. The current stimuli did however invoke perceptual biases in responses. The raw

(individual) responses of both perceptual and motor-based estimates in Experiment 2 were biased by the presence of blur. The biasing of the directly measurable outcomes of both the ventral and the dorsal stream by a stimulus feature processed prior to bifurcation into the two visual streams replicated the earlier findings of Dyde and Milner (2002). Unfortunately the inclusion of a NVS condition was unique to the current research and a comparable condition was not performed by Dyde and Milner (2002). While in agreement with the Dyde and Milner (2002) findings the current research went a step further with the NVS condition and it is hypothesized that had they included the condition their results would mirror those found in the current research. Another potential difference between the Dyde and Milner (2002) study and the current research was their utilization of context-based visual illusions to induce biases in perception and action. Gaussian-like stimuli are generally utilized in the study of vision not as illusory stimuli, but as a means to manipulate detectability (Bijl et al., 1989) and edge-localization (Wilcox et al., 2000). Recently however, it has come to light that Gaussian-like stimuli can under the right conditions result in what has been quantified as a visual illusion (Gori & Stubbs, 2006). The illusory effect has been name the breathing light illusion (or the here comes the sun effect). The illusion can be experienced by fixating on a Gaussian-like stimulus and moving one's head either closer or further from the stimulus. When one moves closer, the stimulus appears bigger and vice versa. The physiological means by which the illusion comes about are currently being investigated (Anstis, Gori, & Wehrhahn, 2007; Gori, Gioria, & Agnostini, 2010). Fortunately for the purposes of the current research the illusory effects only present themselves when the distance between the observer and the stimulus is changing. Unfortunately for Experiment 1 no head restraint was present and as a result the influence of the possible illusion is difficult to quantify. Fortunately it is known that anticipatory postural adjustments are performed to maintain balance during

pointing movements which would result in a high degree of stability during movements (Fits, van der, Klip, Eykern, & Hadders-Algra, 1998). Experiment 2 was protected from breathing light illusion induced biases since participants were seated in a chin rest which held head position constant. Therefore although the use of Gaussian-like stimuli could result in illusory biases, the current experiments were likely robust to the influences of the breathing light illusion.

The findings of Gegenfurtner and Franz (2007) and those presented in Experiments 1 and 2 may also be explained in terms of task-relevant stimulus features. Pointing movements to asymmetrically shaped stimuli are biased in the direction of shifts in the 2D centroid of a stimulus (or centre of mass) (Binsted, Brownell, & Heath, 2008). The high luminance centroid of a 2D Gaussian blob could be interpreted as a very well defined centre of mass. Thus pointing movements to 2D Gaussian blobs should be heavily influenced by the location of the high-contrast centroid while remaining relatively uninfluenced by the ambiguity of the edges. Experiment 1 of the current investigation found that pointing movements scaled equally to changes in size of both solid circles and 2D Gaussian blobs but perceptual estimates of size became increasingly biased by the blobs with increases in size. It is possible that the relevant target stimulus feature for the pointing to the blobs was the high-contrast luminance centroid, which increased proportionally in size with increases in size of the blob. For the perceptual estimates, it is possible that the growing ambiguity of the edges increased bias. Thus, the apparent invariance to the ambiguity of the edges of the Gaussian blobs in the pointing movements could be a byproduct of task-relevant stimulus features scaling with size.

An additional analysis was performed on MT to evaluate the influences of changes in perceived size on MT (see Appendix B). The motivation for the analysis was the previous findings of van Donkelaar (1999) who analyzed MT of pointing movements to the Ebbinghaus

illusion. van Donkelaar found that MT to stimuli that were perceived smaller yielded longer MTs which were in agreement with Fitt's (1954) size scaling. The slopes of MT scaling to changes in size were calculated for each participants for each stimulus class. The slopes were analyzed as a paired samples t-test and found to be not significantly different ($t(11) = -0.92$, $p = .35$) (see Figure A.2). There fore in Experiment 1 both effective target width and MT showed an invariance to increases in edge ambiguity in their scaling to changes in size.

Experiment 2 improved upon Experiment 1 by systematically manipulating the edge blur and the size of stimuli. In addition, by shifting from a pointing task to a grasping task, the edge of the stimulus became a more important task-relevant stimulus feature compared to the centroid of the stimulus. Interestingly, the invariance to blurring of the edges of the stimuli found in Experiment 1 was not replicated. Rather, both the perceptual and motor-based tasks were significantly influenced by increasing blur. Motor estimates scaled uniquely under FVS conditions, but regressed to the degree of scaling exhibited by perceptual estimates under NVS conditions. Thus the biased task-relevant stimulus feature (i.e., the edge), which was available to both visual streams, was represented differentially in the ventral stream (perceptual task) when compared to the dorsal stream (motor task).

The differential pattern of results between Experiments 1 and 2 supports the idea that movements may not have been guided by a singular motor-representation of the stimulus, but by the representation of specific task-relevant stimulus features. The notion of a holistic stimulus representation inherently lends itself more directly to perceptual measures and outcomes. The ventral stream, believed to be primarily responsible for the identification of visual stimuli (Milner & Goodale, 1995), is highly convergent in nature and at the highest levels is required to have assembled object features into a holistic representation. The dorsal stream, on the other hand,

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does not make judgements of identity, but rather it could monitor specific task-relevant target stimulus features to complete a successful movement. In fact, the trajectories of the finger and thumb during grasping movements have been modelled without taking stimulus size into account, but taking the locations of the contact surfaces (edges) of the stimulus into account (Smeets & Brenner, 1999). Therefore a holistic stimulus representation in the dorsal stream could be unnecessary for accurate interactions with stimuli.

The notion of feature specific representations has also been supported by the findings of Jeannerod Decety, and Michel (1994) who examined an individual suffering from optic ataxia found differences between perceptual and motor-implied estimates of size. They concluded that the differences were due to the differential processing of specific stimulus features in the form of visual primitives for the purposes of perceptual-based and motor-based outcomes. If the movement system relied upon a unique holistic stimulus representation, changing a task relevant stimulus feature would necessitate the the re-computation of the stimulus representation. The cost of a re-computation would therefore be expected to be the same regardless of the feature modified. Contrary to that prediction, however, the cost of changing different task relevant stimulus features during an ongoing movement as measured by the latency of the initiation of visually guided adjustments to such changes have been found to differ as a function of the stimulus feature modified. That is, adjustments are made more quickly to changes in stimulus position than to changes in stimulus size (Paulignan et al., 1991a; Paulignan, Jeannerod, MacKenzie, & Martenuik, 1991b). Simply changing a task-irrelevant stimulus feature (colour) has been found to have little influence on movement trajectories, but changing stimulus location as a function of a normally task irrelevant feature (colour) has lead to significant detriment in the ability of an ongoing movement to adjust **(**Cressman et al., 2006). In another experiment, the

modulation of a task-irrelevant stimulus axis (length) negatively impacted the performance of perceptual judgements of width while grasping movements were unaffected (Ganel & Goodale, 2003). And finally, the updating of a holistic stimulus representation for the guidance of movements could result in a negative influence on performance irrespective of the feature manipulated. As that has not been the case, it is concluded that a holistic representation of a stimulus for the guidance of movement is frivolous and unnecessary. Evidence for task specific processing between pointing and grasping has also been found through unique cortical activity during grasping compared to pointing in an fMRI study (Culham et al., 2003). Therefore, a model based upon the guidance of movements to specific task-relevant stimulus features would be a more effective and reactive control system.

Although a model whose motor outputs are governed by representations of stimulus features alone fit with the findings of the current investigation, a re-examination of previous findings was necessary before accepting it as a potential modification to current models regarding unique ventral and dorsal stimulus representations. The introduction of a NVS condition has generally resulted in biased performance in both normal individuals making movements to illusions, and visual-form agnosics making movements to mundane stimuli (Hu & Goodale, 2000; Milner & Goodale, 1995). NVS movements are believed to be governed by a more perceptual representation of the stimuli as the motor representations are believed to exist only transiently (Elliott & Madalena, 1987; Milner et al. 1999; Milner & Goodale, 1995; Westwood & Goodale, 2003). Shifting the point of view to one that is guided by stimulus features explains the data equally well. The representation of the features utilized to guide the movements decay and as such, new stimulus features must be generated from the perceptual representation of the stimulus. In visual-form agnosics, as well as in normal individuals reaching to illusions, the perceptual

stimulus representation is biased or erroneous and subsequent movements generated from the updated representation are also biased. The paradoxical improvements found under NVS conditions in optic ataxics (Milner et al., 1999) can also be explained in a similar manner. Their perceptually mediated stimulus feature set could be interpreted as more accurate than the stimulus feature set the motor system utilizes under FVS conditions. Thus in a NVS condition, the recalculation of stimulus features for the utilization by the motor system could be mediated through the relatively persistent perceptual representation. The utilization of the persistent perceptual feature representation could result in an improvement in motor performance following a delay. Accordingly, an improvement in performance was discovered for motor-based tasks when task-irrelevant background/environmental cues persisted following the removal of the target stimulus (Krigolson & Heath, 2004). This benefit could be explained under the new framework through the utilization of a combination of the more persistent perceptual stimulus representation with the still present background stimuli acting as anchor points to generate more accurate motor-based responses. The final re-examined instances of dissociations between perception and action are demonstrations of movements scaling accurately to non-consciously perceived stimuli (Binsted et al., 2007; Heath et al., 2008). These findings support the notion that stimulus features can be represented in the dorsal stream irrespective of the existence of perceptual representations of the stimulus, and that if no perceptual representation exists, then the motor representation of stimulus features is not overwritten and can still be utilized even following a delay. As all of the previous findings could be easily explained equally by the proposed perspective, motor outputs could be governed by task relevant stimulus features alone, and there is no need for the computation of holistic stimulus representation to accurately guide movements.

Chapter 3: Limitations, Conclusions, and Future Directions

3.1 *Limitations*

One limitation in the current investigation was the amount of modifications that took place between Experiments 1 and 2. The basic concept remained the same in that perceptual estimates were compared with motor based responses but a majority of the details changed. The perceptual estimation changed from a width matching task to a stimulus matching task. The motor task changed from pointing to prehension (grasping). The stimuli flipped contrast. The sizes of the stimuli changed as well. A visual condition manipulation was introduced. The changing of all the different facets make it difficult to perform many meaningful comparisons between the experiments. As an argument to the contrary, all changes between Experiments 1 and 2 were made for the sole purpose at getting a more concise picture of how edges are represented in the outcomes of the two visual streams. Lastly, as both experiments were in fact quite different, but asked similar questions about the human visual system, and got similar answers. This limitation became a strength of the design in that the convergence of the two experiments upon a single conclusion strengthens the conclusion to a greater extent than would have been possible had Experiment 2 changed only one small experimental level.

A second limitation in the current investigations was imposed by the performance of the video hardware used to display the stimuli. The monitor used with the mirror apparatus in experiment 2 failed to properly displaying the entirety of the grayscale palette at high pixel resolution. As a result, the levels of blurring available to the experiment were restricted and only a portion of the grayscale was included in the Experiment 2. The shortfall could be avoided in the future by utilizing better quality display equipment and video-producing hardware in conjunction with the experiment-running computer.

A third limitation was that direct comparisons could not be performed meaningfully between participants because all included factors were repeated in nature. Classical psychophysical paradigms would be required to equate participants on the perceived size and blur of the test stimuli. Such a undertaking would, however prove to be difficult to attain, because equating stimuli upon perceived size between participants would require the on line generation of new stimulus images for each participant. The filtering process used for the generation of the stimuli was computationally intensive, and therefore such a manipulation would not be practically feasible.

A forth limitation was that the length of blurring of stimuli in Experiment 2 exceeded the differences between the sizes of the actual stimuli. Consequently stimuli of a larger size and greater blur appeared smaller than lesser blurred stimuli of a smaller size. This was evident in the measures of variability of responses to the medium sized stimuli being significantly more variable than either of the other two sizes. Keeping the maximum length of blurring smaller than the difference between the sizes of stimuli could result in a data distribution which would not overlap so significantly.

Lastly, a final limitation was that the appropriate means to compare perceptually guided estimates with motor-implied estimates are difficult to assess. Arguments can be made to discount many direct comparison techniques often employed in the literature. The current investigation attempted to rectify this by analyzing the normalized influences of experimentally manipulated variables on the rate of scaling of the outcomes. This was the most appropriate means available, but novel more appropriate means may be soon accepted and available to re-analyze the current data. Also, attempts to equate the two outcome measures often result from a series of data transformations, the direct interpretation of such data can become increasingly clouded which

could result in difficulties in making definitive statements regarding the relationship between perception and action.

3.2 *Conclusions*

In conclusion, the examination of responses of human participants to stimuli with ambiguous edges across the two experiments lent support for the notion of the existence of unique representations of stimulus features governing perceptual and motor-based outcome measures. Of the currently examined models, the Perception-Action model (Milner & Goodale, 1995) was deemed to best explain the data over both the Planning and Control model (Glover, 2004) and the unitary representation model (Franz et al., 2000). Although the Perception-Action model was best supported, the current findings resulted in a proposed adjustment to the model whereby stimulus representations could be viewed as a construct of the ventral/perceptual system, and all of the motor-based data considered both in the current investigation as well as the previous literature could be explained through the representation of task-relevant stimulus features alone. The new interpretation predicted that modulating task-irrelevant stimulus features should not have significant effect of the motor-based interaction with the stimulus unless the task is also altered and the manipulated feature becomes relevant.

3.3 *Future Directions*

Two future studies could be undertaken to help to further distinguish between the possibilities of unique stimulus feature representation in the dorsal stream. The first would compare motor-based outcomes to stimuli whose stimulus features could be manipulated such that the important features for pointing could be independently manipulated from the features important for grasping. One such example stems from the findings that pointing movements tend to be biased by changes in the centre of mass of a stimulus, and thus the location of the centre of mass appears

to be a relevant stimulus feature for pointing. On the other hand, if the location of stimulus edges is an important feature for grasping movements, manipulating edge-location and centre of mass independently would provide a critical test for the model. If a unitary stimulus representation was utilized by the dorsal stream, the trajectories of the movements in both tasks should be equally influenced by the changes in the centre of mass. If only task-relevant features are utilized in the control of the movements, then the grasping trajectories should be invariant to the changes in centre of mass.

The second study would examine the persistence of the motor representations of specific task relevant stimulus features under conditions in which no perceptual representation is present to overwrite the decaying motor-based feature information. Earlier work by Elliott and Madalena (1987) examined the influence of extended delays upon motor outputs in NVS conditions. It was found that no significant decrement was present beyond a 2-30 s delay. The findings were explained by noting that perceptual representations are often stored relatively long term. In the absence of a perceptual representation (e.g., Heath et al., 2008) motor responses continue to scale to target size in a NVS condition. Thus the normal decrement in performance following in a 2-s delay may not be due completely to the decay of the feature representations, but instead due to the existence of a perceptual representation updating the feature representation over time. One could therefore use a paradigm similar to that of a combination of Heath et al. (2008) and Elliott and Madalena (1987) to investigate the true ability of the feature representations to persist over time (tasks relevant or not). One could also examine the type of perceptual and/or motor events could be used to overwrite them. Some potential examples of events would be the presentation of task-irrelevant stimuli or the completion of secondary movements during the delay period. The basic combined paradigm could be described as removing perceptual awareness of a presented

stimulus and requiring participants to wait between zero and twenty seconds before initiating

their response.

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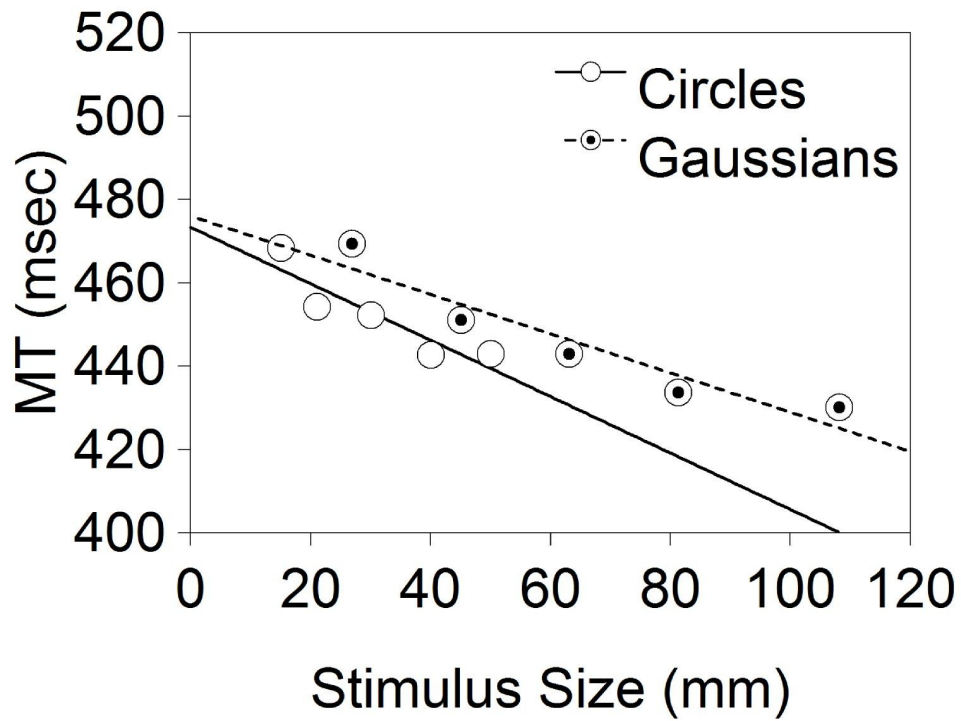
Appendix A: Experiment 1 Additional MT Analysis

Figure A.1: Additional movement time slopes analysis of pointing in Experiment 1. MT scaling

to changes in size of the two stimulus classes did not differ from one another.

Appendix B: Pilot Experiment on Contrast Direction

A number of manipulations were considered to clarify differences found in Experiment 1 between perceptual and motor-implied estimates. One potential source of differentiation was the possibility of unique computation algorithms utilized for edge localization between the visual streams. The utilization of circular objects allowed for a consistent two-dimensional size, and it also introduced curved edges. Working from the assumptions of a second-derivative model for edge localization, the location of a curved edge could be systematically influenced by the direction across the luminance gradient that the edge has been searched for (Mendonca et al., 2004). If the location was estimated by searching down the luminance edge (gradient descent), then increasing blur would result in an inward bias (in the direction the search came from). Conversely, if it the location was determined by searching up the luminance edge (gradient ascent), then increasing blur would result in an outward bias (in the direction the search came from). The possibility that the ventral and dorsal streams could determine edge location in different directions across the luminance profile of a stimulus was assessed in a pilot experiment. Individuals (N = 4) either grasped or made perceptual judgements of size of Gaussian-like stimuli similar to those used in Experiments 1 and 2. The manipulated stimulus feature was the direction of contrast through which the stimuli were defined. Some stimuli were light-on-dark whereas others were dark-on-light. Given that no evidence of an interaction between task and direction of contrast was observed, the manipulation was abandoned (See Figure A.2).
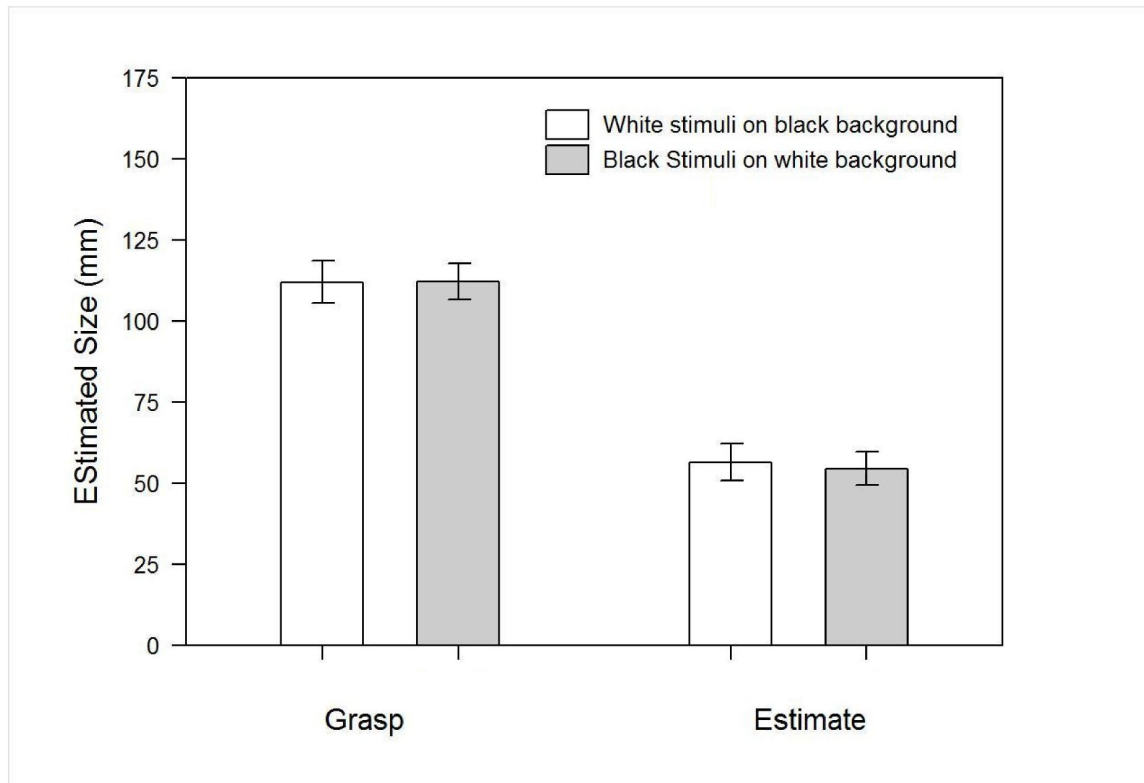
Figure A.2: Pilot experiment: The influence of contrast direction. The direction of contrast change had no effect on the scaling of either motor or perceptual estimates of size. Error bars represent +/- 2SEM.