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**INVESTIGATING THE EFFECTS OF OBJECT CONNECTEDNESS ON RAPID
VISUALLY-GUIDED REACHING TOWARD MULTIPLE GOALS**

(Spine Title: Effects of Object Connectedness on Rapid Reaching)

(Thesis Format: Integrated Article)

by

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Graduate Program in Neuroscience

A thesis submitted in partial fulfillment
of the requirements for the degree of
Master of Science

The School of Graduate and Postdoctoral Studies
The University of Western Ontario
London, Ontario, Canada

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THE UNIVERSITY OF WESTERN ONTARIO
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The thesis by

Jennifer L. Milne

entitled:

**Investigating the Effects of Object Connectedness on Rapid
Visually-Guided Reaching Toward Multiple Goals**

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Master of Science

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Abstract

We developed a rapid reaching paradigm in which we require participants to make speeded reaches toward ambiguous target displays, with a goal target filling-in only after movement onset. In our previous work, we have found that initial reaches extend toward the averaged spatial location of the presented targets. Our aim for the current study was to determine if object connectedness – a strong perceptual illusion in which two connected objects appear as one – could influence the strategic reaching behaviour. Even though there was a powerful effect of the illusion on perception, the visuomotor system was able to utilize the true target information and continue to plan reaches based on the number and distribution of targets presented. These results resonate with the idea of a division of labour between vision-for-perception and vision-for-action – but extend this dissociation (with respect to the action system) into the realm of motor planning.

Keywords: vision, perception, action, reaching, pointing, illusion, gestalt, decision-making, nonsymbolic numerical processing, movement planning, online corrections

Acknowledgement of Co-Authorship

The research included in this thesis is part of an ongoing collaboration with fellow graduate students Craig Chapman, Jason Gallivan, and Daniel Wood, as well as my supervisor Dr. Melvyn Goodale. My collaborators assisted with experimental design and data analysis, while all data collection, displays of results, and written material is my own. My collaborators, particularly Craig Chapman, contributed to the description of functional analyses in the supplemental material as it is included in all of our joint manuscripts.

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Chapter 1

General Introduction

1.1 Introduction

Every moment of every day, we are presented with opportunities for action. Not only must we choose the correct action, but we must also decide exactly how to execute it. It is clear that at some level the brain makes use of environmental information to make such decisions. Currently, there is much debate about the processes and mechanisms underlying such decisions.

1.1.1 Views of Movement Planning

There are two primary perspectives with respect to the decision-making processes underlying action planning and execution. The first reflects typical psychological theories: that the brain acts in a step-by-step manner eventually arriving at a final action decision. From this perspective, the environment is perceived, a decision is made, and an action is performed based on that decision [1]. In other words, a single motor plan is produced for each and every action performed and, if necessary, this single plan is modified if the final target changes [2].

An alternative perspective challenges the typical view on action planning, focusing instead on the possibility that the brain accounts for and encodes multiple potential targets of action in parallel. This view suggests that the brain takes various environmental cues into consideration and uses strategies such as computing probability, costs, and benefits to arrive at a final decision for action [3-6]. In comparison to the single motor plan perspective of action planning, this multiple motor plan account suggests a more flexible view, with the brain weighing all relevant possibilities and shifting seamlessly between different target objects as circumstances change. Given the

vast number of action opportunities and possibilities faced daily, this second perspective may offer a more realistic and efficient view of movement planning.

1.1.2 Multiple Target Encoding in the Brain

The idea of simultaneous encoding of multiple potential targets is one that has received little research attention. Nevertheless, investigations of multiple simultaneous visual representations began with studies of the oculomotor system through the study of saccades [7, 8]. Just as we are often presented with many possible targets for action, we are also faced with many different objects and events that compete for our attention (even before we act). Using single-unit and eye-movement recording, investigators have found that the activity of neurons in the superior colliculus and the trajectories of saccades change according to target probability and the number of potential targets in the environment. This has been interpreted as a way for the oculomotor system to prepare for various possible targets and eventual eye movements. It has been argued, however, that since the eye is a sensory organ, inputs as well as outputs are influenced by visual information [9]. Nevertheless, this initial research on multiple saccade representations provides a strong foundation for investigating the possibility of similar activity in areas of the brain involved in the planning and control of hand and limb movements.

Evidence of this kind of activity in motor areas involved in the planning and control of limb movements has been documented in Cisek and Kalaska's [9, 10] well-known study of the dorsal premotor area of the monkey. This brain region is a high-level motor area in the frontal lobe linked with visuomotor areas in the posterior parietal cortex and with the prefrontal cortex. In both of their studies, the animal was seated in front of a screen displaying one of two tasks: a one-target task or a two-target task. The one-target

task involved cueing a single target location. The display was then removed and after a 500-1500 ms delay, the fixation point changed to the colour of the previously presented target, signaling the monkey to reach toward the proper target location now presented amidst eight possible locations. The two-target task, on the other hand, displayed two possible target locations, where each location was a different colour. The display was then removed and again after a 500-1500 ms delay, the fixation point changed to the colour of one of the two targets, signaling the monkey to reach toward the proper target, again among eight possible locations. The activity in the dorsal premotor cortex was collected throughout the trials in both tasks.

It was found that when two possible targets were presented and the final target remained ambiguous, simultaneous directional signals were generated in different neuron pools in the dorsal premotor area during the delay period, reflecting both of the reach/target possibilities [9, 10]. Once the target became unambiguous, the correct neuronal signals were amplified while the signals for the incorrect target were inhibited. These findings were interpreted as evidence of simultaneous encoding of potential targets of action, clearly contradicting previous sequential views of movement planning.

The present thesis followed on from a line of research in our laboratory that is aimed at pursuing these ideas in humans. As a first step, we developed a behavioural paradigm that we hoped would reflect the activity of dorsal premotor neurons in the human brain.

1.1.3 The Dual Pathway Model of Vision

Before discussing the methods of empirically observing the use of multiple motor plans, it is important to understand which areas of the brain are responsible for such

activity. Rapid, well-practiced actions toward target locations are clearly dependent on vision; the visual system perceives the environment in which the action will take place and specifies the metrics for the action to be properly executed. This process, however, does not take place in a single brain structure. Goodale and Milner [11] have proposed that two separate but interacting visual systems exist within the brain, one responsible for vision-for-perception and one for vision-for-action – the ventral stream and dorsal stream, respectively. The ventral stream, projecting from the primary visual cortex to the inferotemporal cortex, is primarily responsible for perceiving and identifying the lasting characteristics of objects in the surrounding environment. The purpose of the ventral stream, then, is to construct a perceptual representation of the environment, allowing us to identify objects and events in the world. In other words, the ventral stream provides a perceptual foundation for our cognitive life. This vision-for-perception, however, does not directly underlie the implementation of actions, although it does (along with related cognitive mechanisms) play a critical role in the selection of the goal and the actions required to achieve that goal [12].

The purpose of the dorsal stream, on the other hand, is to accommodate the visual information of objects in space and implement actions toward such objects [12]. In other words, the dorsal stream, projecting from primary visual cortex to posterior parietal areas, uses visual information about an object in order to plan and control movements toward that object. The key feature of this dorsal stream is that it registers visual information on a moment-to-moment basis, thus allowing for online control of movements [13]. This is an important difference from the ventral stream. While the ventral stream is processing the enduring properties of an object or target, the dorsal stream continuously registers

visual information about changes in the location or disposition of the object with respect to the observer. This information is useful not only for planning and implementing an appropriate action, but also for making adjustments to an action that has already been initiated [11]. Since the dorsal stream is primarily responsible for the implementation and online control of skilled actions, it is likely that activity underlying multiple action plans would be occurring within dorsal stream areas. At the same time, the identification of multiple goals or targets almost certainly involves ventral stream mechanisms as well. Therefore, the process of encoding multiple potential targets and then selecting the appropriate one is likely to involve an interaction between ventral and dorsal stream mechanisms. Importantly, the dorsal premotor cortex, with its reciprocal connections with both the posterior parietal cortex and prefrontal cortex (which is intimately interconnected with the ventral stream), is well-poised to integrate the activity of the two streams in action planning [for review, see 14].

1.1.4 Parameters of Movement Planning and Control

The task we have developed to test the possibility of multiple-object encoding in humans is a rapid-reaching task towards multiple potential targets where the actual target is revealed only after the movement has begun. But before introducing this task, I will briefly review some relevant areas of research. Finally, I will discuss our findings to date and how those findings have led to the current experiments.

One central feature of our task is online correction of reaching movements, a rapid and ‘automatic’ adjustment of movements that has been shown to be affected by a number of different factors, including the earlier presentation of priming stimuli, the presence of distractors or obstacles, and the probability/expected gain of making a

correction. Masked primes – primes that operate outside of conscious awareness – have been shown to influence pointing trajectories and other kinematic parameters of movements [3, 15]. Directional cues that were presented without the awareness of the participant have been shown to affect motor responses to targets presented overtly, suggesting that the masked prime, although not consciously perceived, was represented at some level during the planning and execution of the movement [16]. Similarly, the size of a masked target was shown to influence the speed with which participants reached out towards that target, indicating the operation of an ‘unconscious’ speed-accuracy trade-off [15]. It is presumed that these effects, which operate outside of awareness, are mediated by visuomotor mechanisms in the dorsal stream.

The presence of obstacles in the workspace has also been shown to influence reach trajectories and increase the need for online corrections. In other words, individuals adjust their trajectories to avoid obstacles as they reach toward the target. Not surprisingly, trajectories are especially affected by obstacles closer to the reaching hand and obstacles that directly obstruct the movement [17]. In addition, reach trajectories have been shown to be affected by objects that are not actually obstacles but instead act as distractors [18]. This suggests that distractors and obstacles are incorporated into the planning and control of the movement [see also, 19]. These findings raise questions as to how the ventral and dorsal streams (together with associated mechanisms in prefrontal and premotor cortex) deal with potential targets versus distractors and obstacles. For the purpose of the current research, however, attention will be focused on the role of multiple potential targets. Nevertheless, knowledge that the brain integrates target and non-target

information is also useful because it supports the notion that multiple encoding of various objects in the environment is taking place during the planning and control of movements.

A final factor that affects reach trajectories and mid-flight corrections involves computations of expected gain and probability. Expected gain refers to a measure of the balance of reward and penalty weighted by their chances of occurring, and has been shown in many investigations to have a significant impact on action decisions. Expected gain is typically represented by analyzing pointing actions toward reward and penalty areas [6, 20, 21]. Research of this type typically involves providing monetary compensation for performance based on touching the reward or penalty areas. Through manipulating the size, location, and number of reward and penalty regions, participants' trajectories and endpoints change in order to produce the greatest chance of obtaining a reward and avoiding a penalty. For example, if only a reward region is presented, the trajectory will extend quickly and with ease toward the middle of the region because success is guaranteed. Alternatively, if the penalty region is large and overlapping with a smaller reward region, the trajectory will extend toward the outermost edge of the reward region (farthest away from the penalty area), attempting to yield success while also avoiding possible contact with the penalty region [6]. Overall, individuals prefer situations with higher expected gain and they use internal estimates of gain – that is, they hedge their bets – in order to make movement decisions. Therefore, there is evidence that individuals use the expected gains of their actions as a strategy to influence the path of their trajectories and also the endpoints of their movements.

Although results of expected gain investigations have shown that the behaviour in these paradigms is nearly optimal, questions arise as to how much the dorsal stream can

perform this kind of computation on its own and how much ventral stream and more cognitive mechanisms are recruited. That is, with presentation of the reward and penalty structure prior to movement onset, are motivation (especially with monetary compensation) and deliberate thoughts and computations coming into play? The possibility that action and endpoint planning may be taking place well before the movement has been addressed by delaying the presentation of necessary target information [4, 6]. Investigations similar to the reward/penalty structure previously discussed have been used to address this issue; the critical difference, however, is that the information which influences the endpoint of the reach is not presented until after the reach has been initiated. Therefore, planning reaches based on expected gain cannot be completed before the onset of the movement; instead, information must be incorporated into the movement plan while the action is already taking place. Despite this delayed presentation of necessary information, participants continued to show the same pattern of movement: maximizing chances of success in reward areas while avoiding proximity to penalty areas [4, 6].

Although delayed onset of information has been shown to influence movement plans and endpoints, the relevant information about the structure of reward and penalty areas must be presented between 200 ms and 400 ms before the endpoint of the movement in order to have an effect [22]. Information presented within this timeframe can be incorporated into the motor plans to make the necessary online corrections to guide the movement in order to successfully arrive at the final target. This means that any study of movement planning to multiple potential targets must present the relevant information to participants at some point between 200 ms and 400 ms between the start

and endpoints of the reaching movement. Information presented before or after this time window would not be usefully incorporated into the movement.

In addition to delayed onset of expected gain information, cues about probability of target locations have been shown to influence reach trajectories before the actual target location becomes clear [4, 5]. Information on possible target location was provided before the onset of the reaching movement, ranging from low to high certainty. When initiating their reach, participants' moved in a direction that reflected those probabilities; when the actual target became clear mid-flight, however, their trajectories had to be shifted in order to successfully complete the task [4]. Overall, previous investigations have shown that information presented not only before movement onset, but also mid-flight impacts the direction of movements and results in the necessity to make online corrections.

All of the aforementioned factors likely involve the activity of the dorsal stream at some level in performing the online corrections. As previously discussed, theory of the dorsal stream proposes that the key role of this vision-for-action area is to implement skilled actions and continually integrate metrical and parameter information in order to make necessary online corrections. From past research, it is evident that having individuals reach toward targets or potential targets and analyzing their trajectories and mid-flight corrections is a clear way to gain insight into the processes and activities of the dorsal stream. At the same time, the use of tasks with multiple targets is likely to reveal how the dorsal stream interacts with other structures, including ventral stream and prefrontal/premotor regions, in the planning of potential movements.

1.1.5 Multiple Target Encoding in Reaching

Based on the parameters of movement planning and control discussed above, we developed a paradigm which requires participants to make rapid reaches toward ambiguous target displays. That is, participants plan and initiate their reach based on displays that have no obvious endpoint at the outset, and it is only after they have initiated their reach that the goal target is cued and their movement must be corrected toward that location. Through multiple experiments utilizing this paradigm, we have found that participants plan and execute strategic reaches toward the ambiguous displays. In other words, they hedge their bets and plan movements that will maximize their chances of success on a given trial [23].

More specifically, we found that when reaching toward a single target presented alone, participants reached directly toward its location. When one target was presented on each side of space, however, instead of arbitrarily choosing one or the other they reached down the middle. This would suggest that each of the individual locations (each with an equal likelihood of becoming the goal target) had its own action plan, and the actual behaviour was a weighted sum of those two action plans, so that the initial trajectory was aimed at the averaged spatial location of the targets, thus maximizing the chances of success. Furthermore, when we changed the ratio of targets on each side of space by adding more targets to one side than the other, we found that initial trajectories were biased toward the side of space with a greater number of targets. Again, this would suggest that each individual target location had its own action plan (or is incorporated into a weighted action plan) and, in order to maximize success (and minimize effort for correcting movements), participants reached toward the averaged spatial location of all

presented targets [23, 24]. These results were consistent with previous research on movement planning involving expected gain discussed earlier [e.g. 6] in that participants adjust their movements based on probability of success and/or failure.

Overall, based on our previous work it is clear that the motor system can incorporate multiple goals during movement planning and execute appropriate actions. What we have yet to determine, however, is the level of involvement of the dorsal and ventral streams in the behaviour elicited through our paradigm. Therefore, the current experiments aimed to determine if a visual illusion known to robustly influence perception would also influence the strategic movements seen in our task.

1.1.6 Visual Illusions

Visual illusion are often a useful way to behaviourally dissociate perception and action. Put simply, illusions can shed light on the processes underlying particular behaviours, as many illusions strongly influence perception while leaving action almost completely immune. In fact, it is these studies that provide the most compelling (although often controversial) behavioural evidence for the dual visual streams theory in healthy populations. For example, when participants view a target circle surrounded by several larger circles, they will perceive the target circle as smaller than when the same target is surrounded by several smaller circles (Ebbinghaus Illusion). When participants are asked to reach out and manually estimate the size of the target circle, however, their estimations are consistent with the veridical size as opposed to the perceived size [25, 26]. Similarly, in the Ponzo (railway track) Illusion, an object placed at the converging end of the display looks larger than a same-sized (or even actually smaller) object placed at the

diverging end of the display; nevertheless, the grip aperture used to pick up the objects reflects the real not the perceived size of the objects [27].

While there are several examples of rapid actions being immune to perceptual illusions, there are also several instances of illusions affecting action [see, for example, 28, 29]. These results do not necessarily refute the idea of two visual streams, however, as many of these apparently contradictory findings can still be explained using the two visual systems account. For example, low-level illusions that are processed early in the primary visual cortex (for example, the stimulus-tilt illusion) will, not surprisingly, influence action (as well as perception), as projections originating in primary visual areas extend to both the ventral and dorsal streams [30, 31]. Therefore, in aiming to dissociate visual perception and action it is crucial to choose an illusion thought to originate later within the ventral stream. Overall, it is important to keep these and other (for example, equating task demands and frame of reference [32, 33]) factors in mind when planning an experiment aimed at dissociating visual action and perception.

Particular properties that underlie many perceptual illusions are those that fall under Gestalt processing. Including different factors such as grouping (including proximity, closure, similarity, etc.), good figure, and continuity, Gestalt properties simply reflect the tendency of the brain to organize objects into patterns, groups or wholes instead of the individual parts [34]. Illusions with these properties are especially useful in the study of visual perception and action as they are encountered in our everyday lives, from perception of faces to making meaningful representations of our surroundings.

The illusion we used in the current study was object connectedness, an illusion based on Gestalt principles that causes two connected objects to be perceived as a single

object. Due to this effect, the presence of connections between objects in a display results in the underestimation of the total number of objects presented [35, 36]. While this effect has been recently shown in perceptual judgements of number, the effect of the illusion on rapid action to multiple targets is yet to be tested. The following chapter will discuss this illusion further.

1.1.7 Motivation for Experiment

Although we have used our versatile paradigm to investigate many aspects of visuomotor planning and control, we are yet to determine what systems are contributing to the behaviour seen in our task. Given the conditions of the experiment (for example, reaches are planned and initiated without the cueing of a goal target), it is possible that ventral stream processes play at least some part in the planning of the movements. Therefore, it would be interesting to see how much perception – in particular, a perceptual illusion – can infiltrate the planning and execution of rapid movements toward multiple goals. The current work used this illusion to determine if object connectedness resulted in underestimation in the motor task, thus influencing how the visuomotor system encodes multiple targets. The findings of these experiments will shed light on the processes underlying the strategic behaviour and determine, at least generally, the contributions of the dorsal and/or ventral streams.

1.2 References

- [1] Shafir, E., & Tversky, A. 1995. *Decision making*. In E.E. Smith and D.N. Osherson (Eds.), *An Invitation to Cognitive Science, Second Edition (Volume 3: Thinking)*. Cambridge, MA: MIT Press, (pp. 77-100).
- [2] Kurata, K. (1994). Information processing for motor control in primate premotor cortex. *Behavioural Brain Research*, *61*, 135-142.
- [3] Cressman, E. K., Franks, I. M., Enns, J. T., & Chua, R. (2007). On-line control of pointing is modified by unseen visual shapes. *Consciousness and Cognition: An International Journal*, *16*, 265-275.
- [4] Hudson, T. E., Maloney, L. T., & Landy, M. S. (2007). Movement planning with probabilistic target information. *Journal of Neurophysiology*, *98*, 3034-3046.
- [5] Trommershäuser, J., Maloney, L. T., & Landy, M. S. (2003). Statistical decision theory and the selection of rapid, goal-directed movements. *Journal of the Optical Society of America, Optics, Image Science & Vision*, *20*, 1419-1433.
- [6] Trommershäuser, J., Landy, M. S., & Maloney, L. T. (2006). Humans rapidly estimate expected gain in movement planning. *Psychological Science*, *17*, 981-988.
- [7] Basso, M. A., & Wurtz, R. H. (1997). Modulation of neuronal activity by target uncertainty. *Nature*, *389*, 66-69.
- [8] McPeck, R. M., & Keller, E. L. (2002). Saccade target selection in the superior colliculus during a visual search task. *Journal of Neurophysiology*, *88*, 2019-2034.
- [9] Cisek, P., & Kalaska, J. F. (2005). Neural correlates of reaching decisions in dorsal premotor cortex: Specification of multiple direction choices and final selection of action. *Neuron*, *45*, 801-814.
- [10] Cisek, P., & Kalaska, J. F. (2002). Simultaneous encoding of multiple potential reach directions in dorsal premotor cortex. *Journal of Neurophysiology*, *87*, 1149-1154.
- [11] Goodale, M. A., & Milner, A. D. (1992). Separate visual pathways for perception and action. *Trends in Neurosciences*, *15*, 20-25.
- [12] Milner, A. D., & Goodale, M. A. (2008). Two visual systems re-viewed. *Neuropsychologia*, *46*, 774-785.
- [13] Goodale, M.A., & Milner, D.A. (2006). One brain--two visual systems. *The Psychologist*, *19*, 660-663.

- [14] Milner, D.A., & Goodale, M.A. (2006). *The visual brain in action*, Second Edition. Oxford: Oxford University Press.
- [15] Binsted, G., Brownell, K., Vorontsova, Z., Heath, M., & Saucier, D. (2007). Visuomotor system uses target features unavailable to conscious awareness. *Proceedings of the National Academy of Sciences*, *104*, 12669-12672.
- [16] Cressman, E. K. (2008). How do invisible stimuli influence action? Visuomotor processing in the absence of conscious awareness. *Dissertation Abstracts International: Section B: The Sciences and Engineering*, *68*, 6947.
- [17] Chapman, C.S., & Goodale, M.A. (2008). Missing in action: The effect of obstacle position and size on avoidance while reaching. *Experimental Brain Research*, *191*, 83-97.
- [18] Tipper, S., Howard L., & Houghton, G. (2000). *Behavioural consequences of selection from neural population codes*. Control of Cognitive Processes: Attention and Performance XVIII. Cambridge, MA: MIT Press
- [19] Song, J., & Nakayama, K. (2006). Control of speed and accuracy set point in visually guided manual-pointing movements. *Visual Cognition*, *14*, 125-128.
- [20] Dean, M., Wu, S., & Maloney, L. T. (2007). Trading off speed and accuracy in rapid, goal directed movements. *Journal of Vision. Special Issue: Sensorimotor Processing and Goal-Directed Movement*, *7*, 1-12.
- [21] Landy, M. S., Goutcher, R., Trommershäuser, J., & Mamassian, P. (2007). Visual estimation under risk. *Journal of Vision*, *7*, 1-15.
- [22] Trommershäuser, J., Mattis, J., Maloney, L. T., & Landy, M. S. (2006). Limits to human movement planning with delayed and unpredictable onset of needed information. *Experimental Brain Research*, *175*, 276-284.
- [23] Chapman, C.S., Gallivan, J.P., Wood, D.K., Milne, J.L., Culham, J.C., & Goodale, M.A. (2010). Reaching for the unknown: Multiple target encoding and real-time decision-making in a rapid reach task. *Cognition*, *116*, 168-176.
- [24] Chapman, C.S., Gallivan, J.P., Wood, D.K., Milne, J.L., Culham, J.C., & Goodale, M.A. (2010). Short-term motor plasticity revealed in a visuomotor decision-making task. *Behavioural Brain Research*, *214*, 130-134.
- [25] Aglioti, S., Goodale, M.A., & DeSouza, J.F.X. (1995). Size-contrast illusions deceive the eye but not the hand. *Current Biology*, *5*, 679-685.

- [26] Haffenden, A.M., Schiff, K.C., & Goodale, M.A. (2001). The dissociation between perception and action in the Ebbinghaus illusion: Nonillusory effects of pictorial cues on grasp. *Current Biology*, *11*, 177-181.
- [27] Ganel, T., Tanzer, M., & Goodale, M.A. (2008). A double dissociation between action and perception in the context of visual illusions: Opposite effects of real and illusory size. *Psychological Science*, *19*, 221-225.
- [28] Franz, V.H., Gegenfurtner, K.R., Bühlhoff, H.H., & Fahle, M. (2000). Grasping visual illusions: No evidence for a dissociation between perception and action. *Psychological Science*, *11*, 20-25.
- [29] Franz, V.H. (2001). Action does not resist visual illusions. *Trends in Cognitive Sciences*, *5*, 457-459.
- [30] Milner, D., & Dyde, R. (2003). Why do some perceptual illusions affect visually guided action, when others don't? *Trends in Cognitive Sciences*, *7*, 10-11.
- [31] Goodale, M.A., Gonzalez, C.L.R., & Króliczak, G. (2008). Action rules: Why the visual control of reaching and grasping is not always influenced by perceptual illusions. *Perception*, *37*, 355-366.
- [32] Bruno, N. (2001). When does action resist visual illusions? *Trends in Cognitive Sciences*, *5*, 379-382.
- [33] Carey, D.P. (2001). Do action systems resist visual illusions? *Trends in Cognitive Sciences*, *5*, 109-113.
- [34] Westheimer, G. (1999). Gestalt theory reconfigured: Max Wertheimer's anticipation of recent developments in visual neuroscience. *Perception*, *28*, 5-15.
- [35] Franconeri, S.L., Bemis, D.K., & Alvarez, G.A. (2009). Number estimation relies on a set of segmented objects. *Cognition*, *113*, 1-13.
- [36] He, L., Zhang, J., Zhou, T., & Chen, L. (2009). Connectedness affects dot numerosity judgment: Implications for configural processing. *Psychonomic Bulletin & Review*, *16*, 509-517.

Chapter 2

Object Connectedness Influences
Perceptual Comparisons but Not the
Planning or Control of Rapid Reaches
to Multiple Goals

2.1 Introduction

Vision plays a significant role in our everyday lives, from perceiving our surroundings to guiding our actions with respect to the objects in our environment. It has been proposed that the processing of incoming visual information takes place along two separate but interacting streams, each arising from primary visual cortex [1]. According to this proposal, the ventral stream – projecting to the inferotemporal cortex – is responsible for the detailed perceptual representation of the objects in our surroundings, while the dorsal stream – projecting to posterior parietal areas – provides the metrics for the flexible moment-to-moment programming and control of visually guided actions such as reaching and grasping.

Initial support for the two visual streams proposal came from neuropsychology [e.g. 2, 3] and neurophysiology [e.g. 4], and, more recently, from functional imaging [e.g. 5, 6]. While sometimes controversial, support for a division of labour between vision-for-perception and vision-for-action has also come from behavioural studies involving pictorial illusions [for review, see 7-9]. One of the most compelling demonstrations of such a dissociation has been demonstrated using the hollow-face illusion, in which a hollow face is seen (incorrectly) as a normal convex face. Króliczak and his colleagues [10] asked participants to use their fingers to ‘flick’ small targets off the actually hollow but apparently normal face. Despite the presence of a compelling illusion of a normal face, the flicking movements were directed at the real, not the illusory locations of the targets. This demonstrates that the visuomotor networks controlling reaching (presumably located in the dorsal stream) can use bottom-up sensory inputs to guide movements to the veridical locations of targets in the real world, even when the perceived positions of the

targets are influenced, or even reversed, by top-down perceptual processing (presumably taking place in the ventral stream).

2.1.1 Object Connectedness

In the current study, we investigated whether or not a similar dissociation exists for a visual illusion involving what is sometimes referred to as ‘object connectedness’. Franconeri, Bemis, and Alvarez [11] showed that estimations of numerosity were affected by the degree of apparent connectedness between adjacent objects in an array. Specifically, pairs of objects (for example, small circles) connected by a line were perceived as a single object as opposed to two separate objects. When several such pairs in an array of circles were connected in this way, the resulting effect was an underestimation of the total number of objects in the display, despite participants being told to ignore any lines and direct their focus only on the circles. While underestimation due to object connectedness was initially found in sequentially presented displays in which one display included connected pairs of circles and the other disconnected circles, the effect has also been shown when the two displays are presented simultaneously [12]. Although the effect of connectedness is stronger with larger set sizes and a greater percentage of connected pairs, the illusion still persists in set sizes with as little as six to ten objects. This is crucial to the current study as all comparisons involve stimuli with six or fewer objects.

It is likely that the connectedness illusion arises because of the brain’s tendency to organize objects into a pattern or whole (otherwise known as Gestalt processing) [for review, see 13]. In other words, even though participants were told to ignore the connection lines, their perceptual system could not help but process the connected pairs

as one as opposed to two separate objects. This grouping tendency in visual perception would appear to be as obligatory as the top-down influences that lead to the perception of a convex face in the hollow-face illusion. But just as target-directed actions can escape the effects of the hollow-face illusion, it is possible that such actions could be refractory to the connectedness illusion. We tested this possibility in the current study by comparing the effects of the connectedness illusion on perceptual estimates of numerosity with the effects of the same illusion on motor planning to multiple targets.

2.1.2 Multiple Action Plans

Neurophysiological findings in monkeys have suggested that neurons in dorsal premotor cortex, which is intimately interconnected with the dorsal ‘action’ stream [14], can simultaneously encode multiple targets in space and thus plan and prepare multiple movements which compete in parallel for execution [15, 16]. Based on this idea, and previous behavioural work that has used reach trajectories to shed light on decision-making processes [e.g. 17, 18], we developed a task in which participants make speeded reaches toward displays with multiple potential targets. Crucially, a goal target is cued only after movement onset; therefore, initial motor planning and execution is based on the ambiguous display. We found that when there was a single target on each side of space, participants initially extended their reaches toward the middle of the two targets and then corrected to the appropriate location when it became apparent. When the ratio of targets in each side of space was not equal, however, the initial reach was biased toward the side of space on which there were more targets [19]. Overall, our previous results have shown that when planning reaches toward multiple potential targets, participants

hedge their bets and reach toward the averaged spatial location of the targets in order to maximize their chances of successfully reaching the goal target.

2.1.3 Current Study

The aim of the current study, then, was to determine whether our rapid reaching task would escape the effects of object connectedness or whether it would show the same sensitivity to object connectedness as perceptual comparisons of numerosity. In other words, would the trajectories of the reaching movements be less ‘attracted’ to the side with more potential targets if those targets were interconnected. The results were clear. Despite the fact that perceptual judgements were strongly influenced by the presence of connecting lines between the targets (connected displays were perceived as having fewer targets than disconnected ones), we found no influence of object connectedness on the reach trajectories. Even in the presence of connections, participants continued to make strategic reaches based on the actual number of targets.

2.2 Methods

2.2.1 Participants

A total of 30 participants (mean age: 22.5 years, 18 females) were recruited from the University of Western Ontario (London, Ontario, Canada) to take part in both the perceptual and the rapid reaching task. All participants were right-handed, as determined by the Edinburgh handedness questionnaire [20], and had normal or corrected-to-normal vision. Informed consent was obtained in accordance with procedures approved by the University’s Psychology Review Ethics Board. Seven participants were excluded from analysis because they failed to meet the timing constraints for performance on the tasks

(see Supplemental Material for description of removal procedures). All participants received monetary compensation for their participation.

2.2.2 Apparatus and Stimuli

Participants were seated comfortably at a table for the duration of the experiment. Target displays were presented on a 40-in touch screen (NEC MultiSync© LCD4020) and were controlled using custom Matlab software (version 6.5) with the Psychtoolbox (Version 2, 1, 2). For the perceptual task, voice onset was recorded using a microphone placed in front of the participant and the participant's response was recorded by the experimenter. For the reaching task, trajectories were recorded (at 150 Hz) via an OPTOTRAK motion tracking system (Northern Digital Inc., Waterloo, Canada) using two infrared emitting diode (IRED) markers placed on the index finger of the right hand (one on the tip, the other directly behind it). Marker wires were held in place with a wrist band to allow for unrestricted movement of the arm. There were also three stationary IREDs placed on the touch screen.

Target displays consisted of groups of two, four, or six small circles (1 cm radius, hollow black circle on a white background) on both the left and right side of fixation. The circles in the displays on each side of space were either connected to a neighbouring circle by a small line (1 cm) in sets of two or were disconnected. Disconnected circles had half of a connection line (0.5 cm) at one of the possible connection directions without allowing any pairs to be made. The displays on each side of space were either all connected in pairs or all disconnected. Therefore, there were four levels of connectedness: display on left connected (with display on right disconnected), display on right connected (with display on left disconnected), displays on both sides of space with

connections, and displays on both sides of space with disconnections (see Figures 2-2, 2-3, and 2-4 and Supplemental Figures for example displays). Some trial types were not included either because it was difficult to connect the targets with 1-cm lines or because the comparison between the left and right displays would not generate a reliable underestimation (see Supplemental Material and Supplemental Figure 2-7 for further details concerning the stimuli and apparatus).

2.2.3 Procedure

Trials began with the participant viewing a black fixation cross (centered on the touch screen) for a variable delay with their right index finger on the start button. The fixation screen was then replaced by one of the possible target displays. At the same time, an audio cue ('beep') was presented which instructed participants to release the button. Immediately following the release of the button, one of the targets in the display filled-in black. Importantly, each potential target had an equal probability of filling in upon release of the start button. For the perceptual task, participants were required to indicate if the side of space on which the black circle appeared contained a greater number of circles or fewer circles than the opposite side through a verbal response (by saying "more" or "less", respectively). For the reaching task, participants had to rapidly reach toward the touch screen and put their fingertip on the cued target location. The goal target appeared an equal number of times on each side of space to control for the effects of any side bias [21]. Crucially, participants were told to ignore all lines and focus only on the circles. At the end of each trial, feedback was displayed on the touch screen related to timing constraints or location touched on the screen (reaching task only). Participants were given

the opportunity to learn and practice both tasks before data acquisition began. See Figure 2-1 and Supplemental Figure 2-7 for further details.

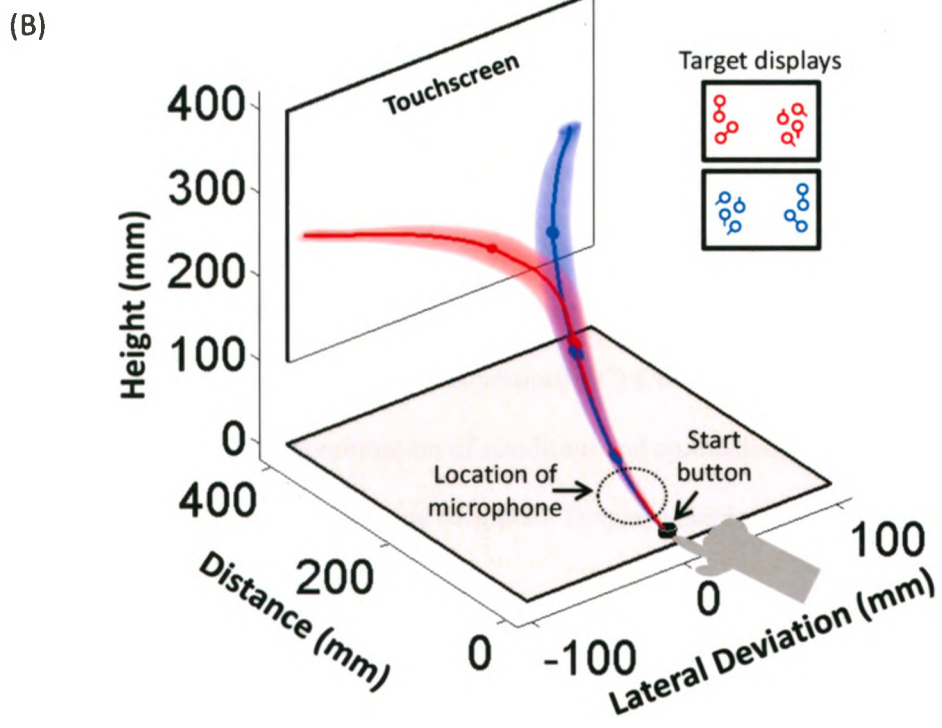
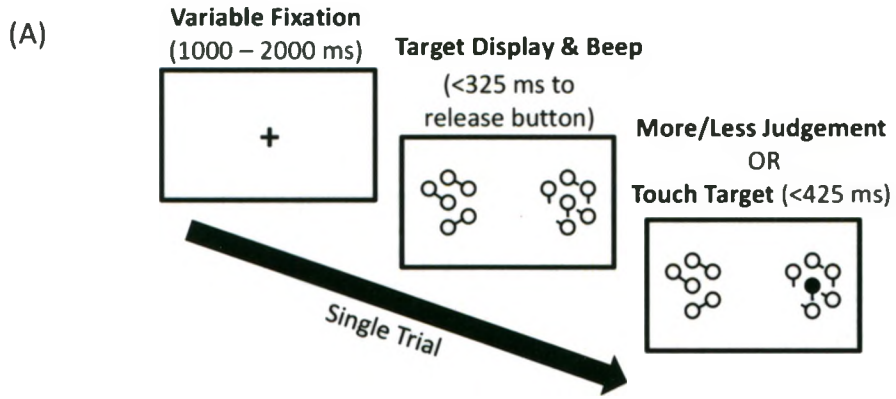
2.3 Results

2.3.1 Perceptual Task

Responses in the perceptual task were analyzed using a 7 (condition) x 4 (connectedness) x 2 (cue-side) repeated-measures analysis of variance (ANOVA) (see Figure 2-2 for an example of the levels included in each factor). The analysis compared only the number of “less” responses for all possible comparisons in the ANOVA. Since there were always five repetitions of all trial types, the significance levels for the “more” responses could be inferred from the results of the ANOVA carried out on the “less” responses.

The analysis revealed a significant interaction of condition and connectedness ($F(8.36, 183.91) = 13.51, p < .001$), and posthoc analyses (Bonferroni corrected) revealed that connectedness resulted in an underestimation of the true number of targets in the display. That is, in cases where target number was equal on each side of space, the presence of connections on one side of the display resulted in an underestimation of that side ($ps < .01$). Similarly, for trials with an unequal number of targets on each side, the presence of connections on the side with more targets resulted in an underestimation of that side; in other words, participants treated these trials in the same way they treated baseline trials (both sides of space with connections or disconnections) in which target numbers were equal ($ps < .01$). Data from select comparisons are shown in bar graphs in Figures 2-3 and 2-4, as well as Supplemental Figures 2-5 and 2-6. Post hoc results for all comparisons can be found in Supplemental Table 2-1. Main effects of condition

Figure 2-1. (A) **Trial Timing:** For both tasks, participants began by fixating a cross for a variable time interval (1000-2000 ms) while holding their right index finger on the start button. The target display replaced the fixation screen and was accompanied by an audio cue signaling participants to release their finger off the start button (within 325 ms). Upon releasing the start button, one of the circles on the screen filled-in black and participants were asked to indicate if that side had a greater number of circles or fewer circles than the other side (by verbally indicating “more” or “less”, respectively) (perceptual task) or reach to touch that location (reaching task) (responses required within 425 ms). (B) **Apparatus:** Display indicating location of table, touch screen, and start button. For perceptual task, a microphone was placed directly in front of the start button. Target displays are not drawn to scale.



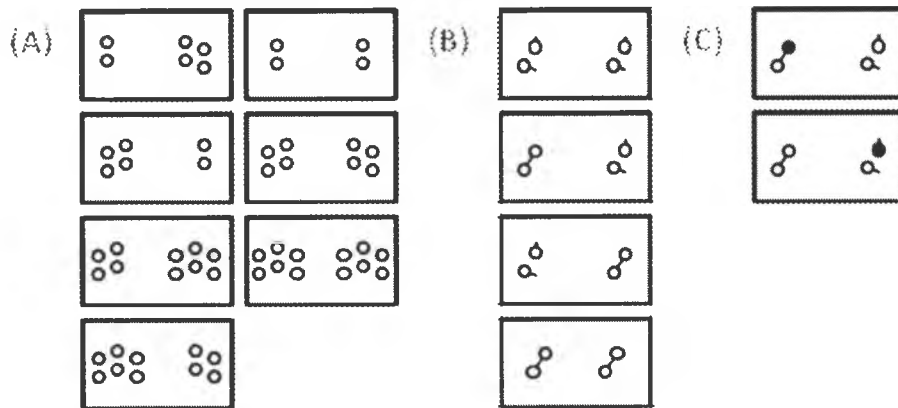


Figure 2-2. Schematic of factors included in the analysis of variance. (A) **Condition:** defined by the number and spatial distribution of potential targets. (B) **Connectedness:** defined by the location of connection/disconnection lines (the four levels of connectedness apply to each level of condition). (C) **Cue-side:** defined by location of goal target (within each combination of condition and connectedness, the goal target can appear in either the left or right side of space). Displays are not drawn to scale.

($F(6, 132) = 134.79, p < .001$) and connectedness ($F(3, 66) = 304.73, p < .001$) were also found. Given the significant interaction between the factors, however, these results must be interpreted with caution and are not presented. The analysis revealed no effect of cue-side ($p > .05$), suggesting the position of the goal target (and thus the side of space that became the reference) did not play a factor in how participants responded. In summary then, connectedness had a strong and reliable effect on perceptual estimations of numerosity.

2.3.2 Reaching Task

For analysis of the reaching task, we used functional data analysis techniques to fit mathematical functions and to spatially normalize the reach trajectories (see Supplemental Material). We then used functional analyses of variance (FANOVAs) to compare the trajectories of the trials of interest. The use of FANOVA is especially useful for this analysis as it shows not only if, but also where and to what magnitude the particular trajectories differ. In Figures 2-3 and 2-4, we use significance bars to indicate the significant differences for the particular trajectories, with the colour-intensity of the bar at each point denoting the magnitude of the difference at that specific point. The absence of significance bars indicates the lack of any significant differences between trajectories across the entire movement.

The effects of the different target configurations on reach trajectories are best seen by viewing the entire movement (see Figures 2-3 and 2-4). We replicated our previous findings and showed that when the target ratio was equal, reaches extended down the middle before correcting to the goal location. When the ratio was not equal, however, reaches were biased toward the side where there were a greater number of targets. These

Figure 2-3. Above view of averaged reach trajectories are presented for baseline and left-side-connected conditions when the goal target appeared on the left side of space. Example displays are shown for each corresponding plot (displays are not drawn to scale). Solid black horizontal bar indicates location of touch screen. Shading around each trajectory represents the average standard error across subjects, with spheres at 25%, 50%, and 75% of reach distance proportional to the velocity in each dimension. Black gradient bars indicate the magnitude of the difference between the trajectories at any given point. Bar graphs display average percentage difference between the number of 'more' and 'less' responses for each trial type in the perceptual task. Bars extending in the negative direction signify a greater proportion of 'less' responses, and bars extending to the right signify a greater proportion of 'more' responses. Asterisks indicate a significant difference at an alpha of at least .01.

Significance Bars

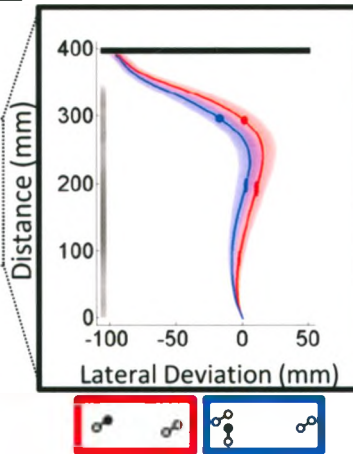
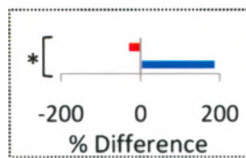
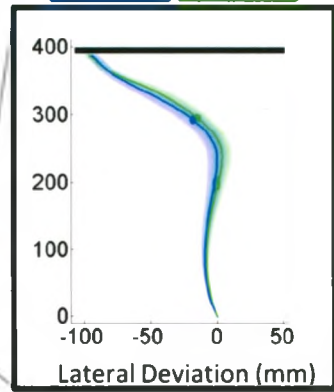
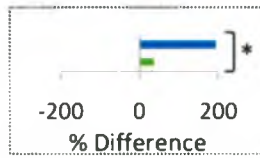
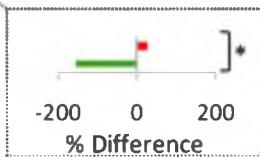
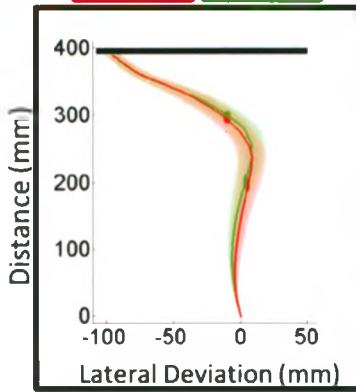
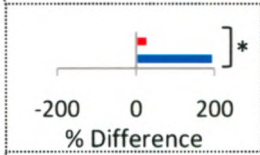
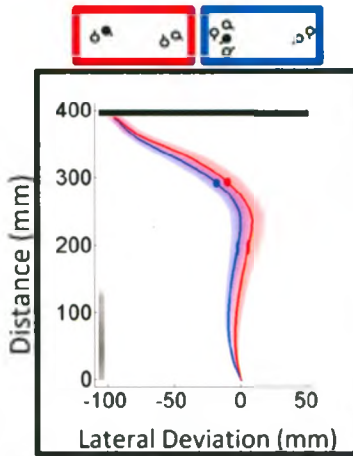
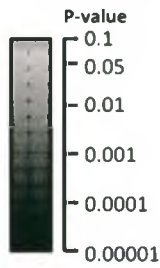
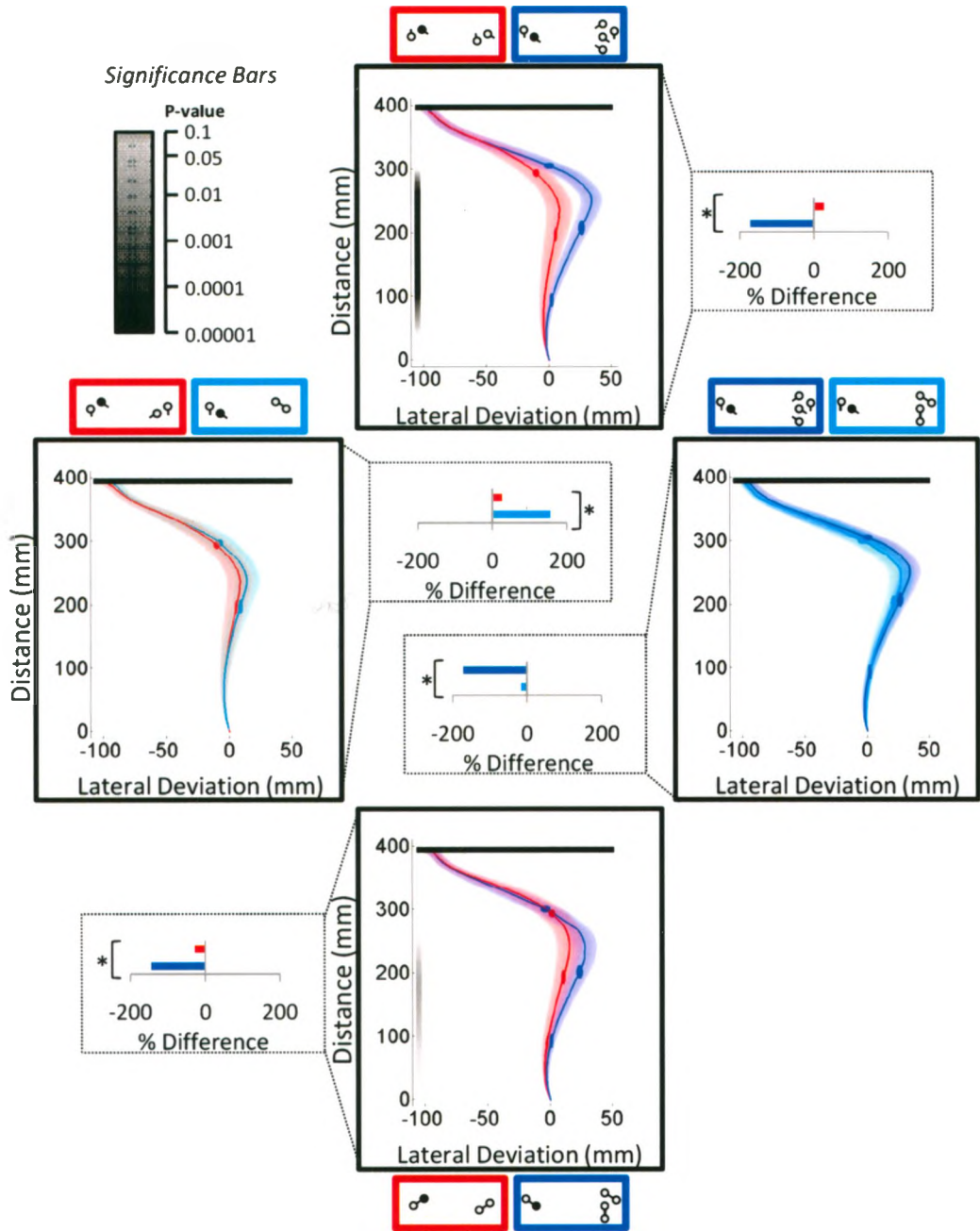


Figure 2-4. Above view of averaged reach trajectories are presented for baseline and right-side-connected conditions when the goal target appeared on the left side of space. Example displays are shown for each corresponding plot (displays are not drawn to scale). Solid black horizontal bar indicates location of touch screen. Shading around each trajectory represents the average standard error across subjects, with spheres at 25%, 50%, and 75% of reach distance proportional to the velocity in each dimension. Black gradient bars indicate the magnitude of the difference between the trajectories at any given point. Bar graphs display average percentage difference between the number of 'more' and 'less' responses for each trial type in the perceptual task. Bars extending in the negative direction signify a greater proportion of 'less' responses, and bars extending to the right signify a greater proportion of 'more' responses. Asterisks indicate a significant difference at an alpha of at least .01.



effects are seen in the baseline plots (in cases where both sides of space were disconnected or when both sides had connections). When cycling through the different levels of connectedness within particular conditions, however, we found no differences in the trajectories. That is, despite the presence of connections on the left or right side, participants behaved as they did in baseline trials. See Supplemental Figures 2-5 and 2-6 for reaches with an endpoint on the right side of space.

Although we show only those conditions that correspond to our most replicated findings, it is important to note that object connectedness had no effect on reaches toward all other trial types. Overall, despite a robust effect of object connectedness on perceptual comparisons, participants were able to rapidly plan and execute strategic reaches based on the veridical number of targets, even in the presence of connected pairs in the displays. For analysis of kinematic measures see Supplemental Material and Supplemental Table 2-3.

2.4 Discussion

The current study investigated whether object connectedness – a strong perceptual illusion in which two connected objects appear as one – would influence rapid reaches sensitive to target number. Although we found a clear and robust effect of the illusion on perceptual comparisons, the results revealed no effect of the illusion on action. The analysis of the reach trajectories provided a replication of our previous work, showing that in conditions with no connected pairs, reach trajectories were biased toward the averaged spatial location of the potential targets. Remarkably, participants behaved exactly the same way with connected targets. Despite the presence of a perceptual illusion due to connected targets, the visuomotor system coded the actual number of

targets presented, and then planned and executed the reaches accordingly. This means that the visuomotor system must either have access to alternate sources of visual information or must deal with the visual information in a way that is quite different from the perceptual processing that creates the illusion. These results resonate with the two visual streams theory [1] but extend these ideas into the realm of motor planning.

One concern we had when planning the current experiment was whether or not pictorial illusions would influence stimuli within the subitizing range. Subitizing is the fast and accurate enumeration of small set sizes (the exact range is debatable, but it is typically thought to be 1 to 4) [22]. Because subitizing is thought to be controlled by pre-attentive processes, it has been assumed that it cannot be easily compromised or disrupted [23]. More recent research, however, has suggested that subitizing is not pre-attentive and can indeed be disrupted by differences in attentional demands [24, 25]. In other words, attentionally demanding tasks disrupt subitizing and participants revert to other ways of estimating number, such as counting [24]. Based on these findings, it is entirely possible that the same variables that affect counting could still operate in the subitizing range, but perhaps with less force and precision, and only in attention-demanding tasks. The fact that we found a robust effect of the connectedness illusion in the subitizing range suggests that perhaps our experiment was so attentionally demanding that the illusion could be effective even with small set sizes.

The rapid-reaching task that we used offers the unique opportunity not only to examine real-time continuous movements, but also to address several questions that are currently posed in the action-perception literature. For example, by viewing all stages of the movement, we were able to demonstrate that participants (1) were not simply moving

blindly toward the touch screen until the goal target was cued, (2) were not initially fooled by the connectedness illusion and then later adjusting their movements in-flight, but (3) were able to correct their movements properly in-flight. The latter two points directly contradict previous research that suggested visual illusions compromise both movement planning and online corrections [26, 27]. Instead, our results indicate (at least as far as the connectedness illusion is concerned) that the visuomotor system plans movements accurately very early on, despite the fact that goal selection may be based on a perceptual representation. In our task, of course, because the final target was not cued until after movement onset, the role of perception was to select the entire set of targets as the ‘goal’. But the fact that the connectedness illusion did not affect movement planning suggests that the movements to each of the potential targets were somehow computed independently from the perceptual selection. This fact strongly supports the idea that each individual target was being prepared for action and not simply represented perceptually – and suggests that other studies that have used pictorial illusions need to be re-visited to see if this distinction between goal selection and movement planning operates there as well [for a discussion, see 28].

A particular criticism of the use of visual illusions to dissociate perception and action is that the task demands are not equated, and therefore the same processing does not underlie both responses. For example, it has been suggested that action is immune to illusions because the motor response requires the processing of only the target, while perception involves the processing of the entire display [29]. Our paradigm, however, directly addresses this criticism as participants are required to view and process the entire display in both tasks; after all, the final target remains ambiguous until the initiation of a

response. In the perceptual task, all potential targets must be enumerated in order to make a comparison of magnitude. Similarly, in the reaching task, all potential targets must be represented for action as each location had an equal likelihood of becoming the goal target. Therefore, not only were our tasks matched on general demands (for example, timing constraints, button release, target-cue onset, etc.), the response demands for both tasks required the processing of the entire display.

In summary, our results provide compelling support for a sharp dissociation between vision-for-perception and vision-for-action. But beyond this, our results suggest that the perceptual processes underlying goal selection are distinct from those processes underlying the planning of movements towards those goals – even though these processes must operate in parallel.













2.5 Supplemental Materials













2.5.1 Additional Data and Analyses













2.5.1.1 Perceptual and Reaching Task













Results from the analysis of perceptual responses for all trial types are shown in Supplemental Table 2-1. Additional trajectory results are presented in Supplemental Figures 2-5 and 2-6, showing performance for goal targets on the right side of space. The effect of the illusion on perceptual judgements was robust, regardless of the number and distribution of potential targets, connectedness, or the side of space on which the cue was presented. Although the differences in reach trajectories decreased with increasing number of targets, we nevertheless found that object connectedness had no effect on the reaches and participants continued to plan and execute movements based on the actual number of targets.













Supplemental Table 2-1. Posthoc comparisons of perceptual responses for all trial types. Responses included in the analysis were “less” responses only. Therefore, a significant result indicates that there was a difference between the number of “less” responses for that particular comparison (i.e. participants were not equally confident that there were fewer circles in the respective side). Significant differences expected based on the hypotheses are bolded. Displays are not drawn to scale.













| Cue-Side |   | |   | |   | |
|---|---|------|---|------|---|------|
| | L | R | L | R | L | R |
|   | .256 | .971 | .621 | .054 | .000 | .000 |
|   | .000 | .000 | .000 | .007 | | |
|   | 1.00 | .014 | | | | |













| Cue-Side |   | |   | |   | |
|---|---|------|---|------|---|------|
| | L | R | L | R | L | R |
|   | .000 | .000 | .000 | .000 | .000 | .000 |
|   | .000 | .000 | .000 | .000 | | |
|   | .194 | .374 | | | | |

| Cue-Side |   | |   | |   | |
|---|---|------|---|------|---|------|
| | L | R | L | R | L | R |
|   | .000 | .000 | .000 | .001 | .000 | .004 |
|   | 1.00 | 1.00 | 1.00 | 1.00 | | |
|   | 1.00 | .149 | | | | |

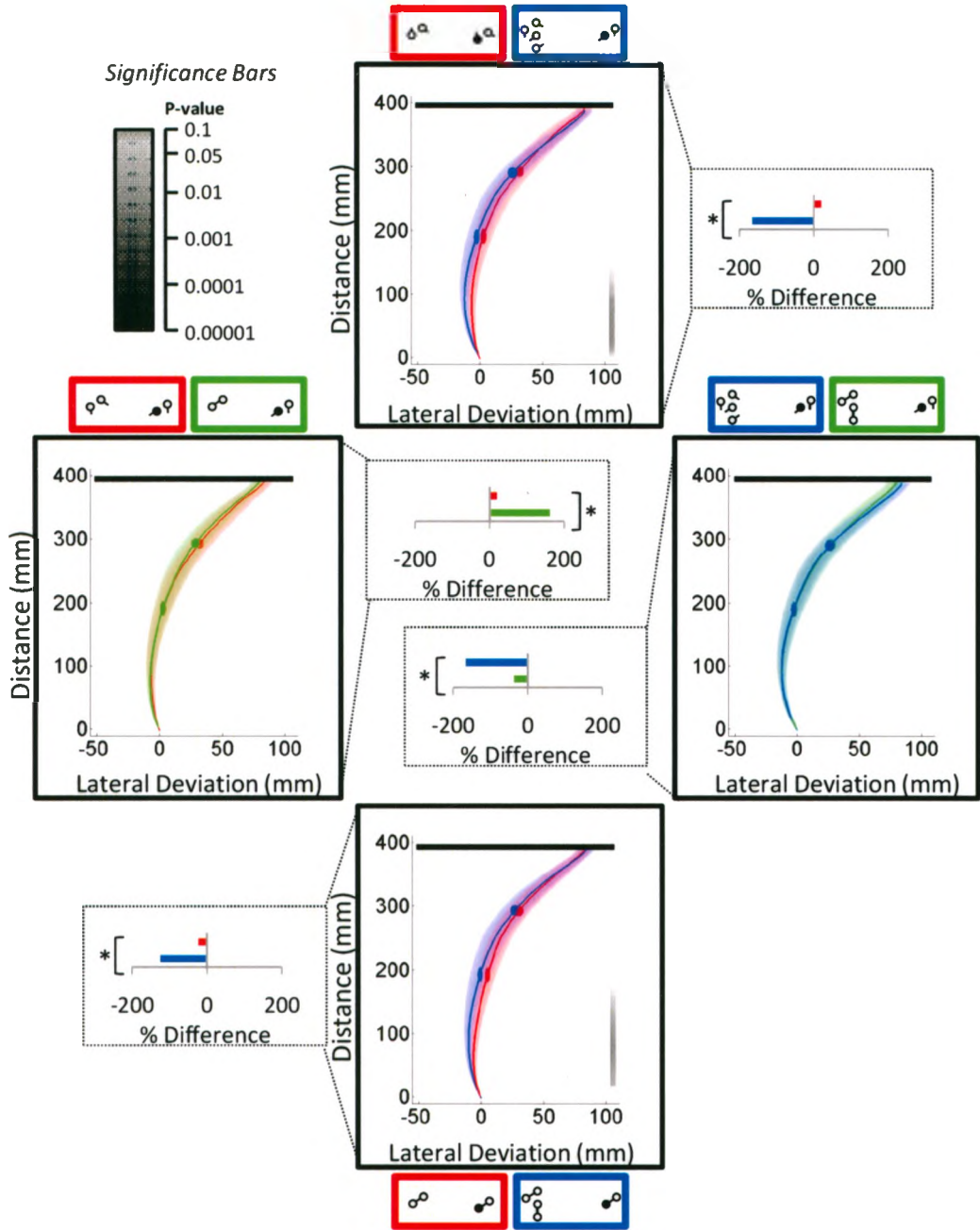
| Cue-Side |   | |   | |   | |
|---|---|------|---|------|---|------|
| | L | R | L | R | L | R |
|   | .000 | .001 | .010 | .000 | .000 | .000 |
|   | .000 | .000 | .000 | .000 | | |
|   | 1.00 | .174 | | | | |

| Cue-Side |   | |   | |   | |
|---|---|------|---|------|---|------|
| | L | R | L | R | L | R |
|   | 1.00 | .971 | 1.00 | .088 | .000 | .000 |
|   | .000 | .000 | .000 | .000 | | |
|   | 1.00 | .436 | | | | |

| Cue-Side |   | |   | |   | |
|---|---|------|---|------|---|------|
| | L | R | L | R | L | R |
|   | .000 | .000 | .000 | .000 | .000 | .000 |
|   | .001 | .000 | .000 | .000 | | |
|   | .436 | .013 | | | | |

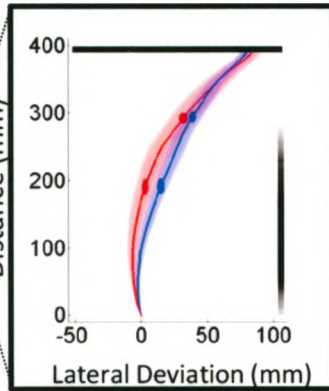
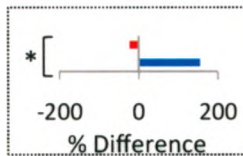
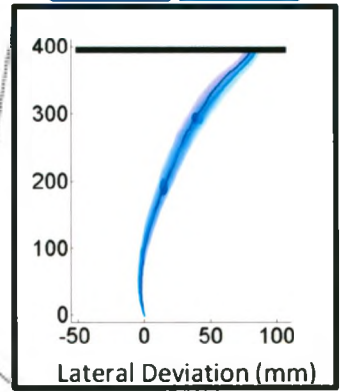
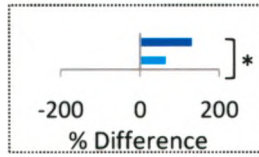
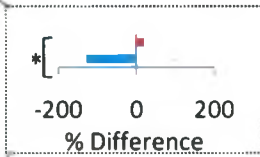
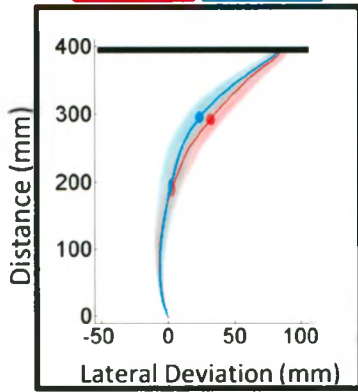
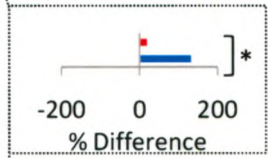
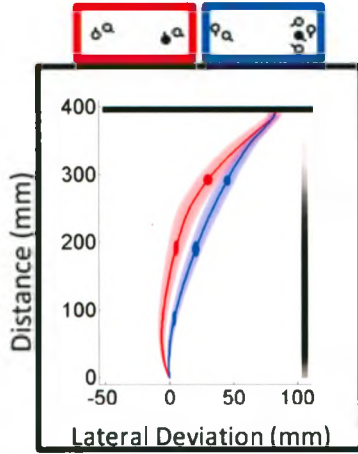
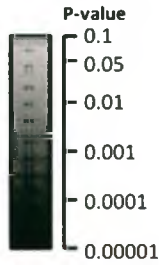
| Cue-Side |   | |   | |   | |
|---|---|------|---|------|---|------|
| | L | R | L | R | L | R |
|   | .000 | .000 | .000 | .000 | .000 | .000 |
|   | 1.00 | .008 | .054 | .283 | | |
|   | .298 | .498 | | | | |

Supplemental Figure 2-5. Above view of averaged reach trajectories are presented for baseline and left-side-connected conditions when the goal target appeared on the right side of space. Example displays are shown for each corresponding plot (displays are not drawn to scale). Solid black horizontal bar indicates location of touch screen. Shading around each trajectory represents the average standard error across subjects, with spheres at 25%, 50%, and 75% of reach distance proportional to the velocity in each dimension. Black gradient bars indicate the magnitude of the difference between the trajectories at any given point. Bar graphs display average percentage difference between the number of 'more' and 'less' responses for each trial type in the perceptual task. Bars extending in the negative direction signify a greater proportion of 'less' responses, and bars extending to the right signify a greater proportion of 'more' responses. Asterisks indicate a significant difference at an alpha of at least .01.



Supplemental Figure 2-6. Above view of averaged reach trajectories are presented for baseline and right-side-connected conditions when the goal target appeared on the right side of space. Example displays are shown for each corresponding plot (displays are not drawn to scale). Solid black horizontal bar indicates location of touch screen. Shading around each trajectory represents the average standard error across subjects, with spheres at 25%, 50%, and 75% of reach distance proportional to the velocity in each dimension. Black gradient bars indicate the magnitude of the difference between the trajectories at any given point. Bar graphs display average percentage difference between the number of 'more' and 'less' responses for each trial type in the perceptual task. Bars extending in the negative direction signify a greater proportion of 'less' responses, and bars extending to the right signify a greater proportion of 'more' responses. Asterisks indicate a significant difference at an alpha of at least .01.

Significance Bars



2.5.1.2 *Reaction/Response Time Analysis for Perceptual Task*

Reaction times (button-release) and voice onset times were recorded during the perceptual task to determine if particular conditions or levels of connectedness had an effect on participants' response times. Each of the variables were submitted to a three-factor (7x4x2: condition (number of potential targets in display) x connectedness x cue-side (target appearing on left or right)) repeated measures analysis of variance (ANOVA). The analysis revealed no significant interactions or main effects of reaction time, suggesting that our task was successful in inducing rapid reaction times regardless of the display presented.

The analysis of voice onset time revealed only a significant main effect of connectedness ($F(2.35, 46.67) = 2.83, p < .05$, Greenhouse-Geisser corrected), with participants responding faster to baseline trials (both sides with connections or with disconnections) than to trials with connections on either the left or right side. ($ps < .05$). The reason for this difference in response time is not clear – although it may be the case that the difference in the visual appearance of the connected and unconnected stimuli resulted in some sort of processing cost or conflict. See Table 2-2 for means corresponding to all trial types.

2.5.1.3 *Kinematic Analysis*

We calculated participant averages on five dependent measures across all trial types in order to determine if any effects of connectedness could be seen on the temporal component of the reaches:

Reaction Time (ms): Time from the start of the trial (audio cue) to the button release.

Supplemental Table 2-2. Means for reaction time (RT, ms) and voice onset time (VOT, ms) of responses in the perceptual task. Displays are not drawn to scale.

| Target on Left | | | Target on Right | |
|----------------|--------|--|-----------------|--------|
| RT | VOT | | RT | VOT |
| 228.31 | 389.13 | | 228.42 | 388.23 |
| 227.96 | 393.49 | | 227.34 | 391.34 |
| 229.04 | 394.18 | | 227.98 | 393.89 |
| 228.47 | 388.87 | | 228.63 | 389.74 |
| 229.39 | 387.48 | | 229.06 | 386.20 |
| 229.04 | 395.73 | | 228.01 | 389.79 |
| 228.83 | 393.45 | | 228.74 | 390.15 |
| 227.70 | 389.31 | | 229.80 | 387.22 |
| 229.31 | 388.03 | | 227.21 | 388.40 |
| 228.96 | 393.97 | | 228.42 | 392.63 |
| 230.01 | 395.87 | | 227.30 | 394.90 |
| 229.46 | 390.11 | | 229.03 | 388.96 |
| 229.81 | 389.35 | | 227.37 | 387.46 |
| 228.93 | 395.07 | | 228.02 | 391.86 |
| 230.11 | 394.66 | | 228.14 | 392.79 |
| 227.91 | 387.91 | | 227.98 | 388.60 |
| 229.13 | 386.18 | | 227.91 | 387.01 |
| 227.36 | 390.31 | | 228.44 | 391.00 |
| 227.13 | 391.47 | | 227.28 | 391.82 |
| 228.12 | 387.33 | | 227.99 | 388.88 |
| 229.36 | 387.50 | | 228.13 | 387.97 |
| 227.84 | 391.73 | | 227.87 | 394.90 |
| 228.14 | 392.94 | | 228.93 | 392.19 |
| 227.07 | 389.01 | | 227.88 | 387.92 |
| 229.83 | 388.07 | | 228.45 | 389.18 |
| 228.19 | 394.80 | | 230.12 | 395.28 |
| 228.56 | 395.14 | | 229.83 | 393.97 |
| 230.45 | 389.23 | | 229.01 | 388.41 |

Movement Time (ms): The time between button release and contact with the touch screen.

Peak Velocity (mm/s): The highest vector velocity during the reach.

Time to Peak Velocity: Time from the start of the movement until peak velocity.

Percent Time to Peak Velocity (%): The Time to Peak Velocity expressed as a percentage of Movement Time.

Each of the above five measures were submitted to a three-factor (7x4x2: condition x connectedness x cue-side) repeated measures ANOVA to test for differences in the temporal components of the reaches. All results are reported with Greenhouse-Geisser correction for sphericity. For ease in interpretation, the following is a list of the displays that fall under the factor 'condition' (with each condition being further subdivided into four levels of connectedness):

| | | |
|-------------|--|--|
| Condition 1 | ○ _o | ○ _o ○ _o |
| Condition 2 | ○ _o ○ _o | ○ _o |
| Condition 3 | ○ _o ○ _o | ○ _o ○ _o ○ _o ○ _o |
| Condition 4 | ○ _o ○ _o ○ _o ○ _o | ○ _o ○ _o |
| Condition 5 | ○ _o | ○ _o |
| Condition 6 | ○ _o ○ _o | ○ _o ○ _o |
| Condition 7 | ○ _o ○ _o ○ _o ○ _o | ○ _o ○ _o ○ _o ○ _o |

For reaction time, only a significant main effect of condition was found ($F(4.56, 104.98) = 4.12, p < .01$), with condition five (two targets on each side) differing significantly from condition three (four targets on one side and six on the other) and condition seven (six targets on each side), $ps < .05$. This is likely due to differences in

total target number (and thus differences in uncertainty) between the conditions.

Although some minor differences were found, the absence of substantial differences is consistent with our previous work [19, 21] as our task demands rapid responses regardless of trial type.

For movement time, only a main effect of cue-side was found ($F(1, 22) = 68.14, p < .001$), with all reaches to the right being faster than those to the left ($ps < .001$). This is consistent with our previous work and is likely due to biomechanical constraints of the right arm as all participants were right-handed.

In the analysis of peak velocity, only a main effect of cue-side was found ($F(1, 22) = 21.44, p < .001$), with reaches to the left having a higher peak velocity than those to the right. Similarly, the analysis of time to peak velocity revealed a significant main effect of cue-side ($F(1, 22) = 84.47, p < .001$), again with reaches to the left reaching peak velocity in a shorter period of time than reaches to the right.

Finally, the analysis of percent time to peak velocity revealed a significant interaction of condition and connectedness ($F(8.76, 201.46) = 1.95, p < .05$), with differences found only within condition four (six targets on the left and four on the right). When there were disconnections on both sides, participants spent more time accelerating than when both sides were connected ($p < .05$). An interaction was also found between condition and cue-side ($F(3.74, 86.04) = 2.74, p < .05$), with reaches toward conditions two and four spending less time accelerating than in condition six when the target was on the left ($ps < .01$) Finally, a main effect of cue-side was found ($F(1, 22) = 158.31, p < .001$), with participants spending more time accelerating when the final target appeared

on the left. This result, however, can be interpreted only in light of the interaction of condition and cue-side.

The results of the analyses on velocity measures are consistent with longer movement times toward the left, suggesting that although the movements accelerated quickly in the beginning phase (when the goal target location was still ambiguous), there was a deceleration in the correction phase. This resulted in longer movement latencies, a finding which is consistent with existing literature on corrected movements [see, for example, 30]. In addition, participants spent a greater percentage of their movement reaching peak velocity when the target filled-in on the left side. Overall, these longer latencies toward the left are similar to those reported in our previous work, suggesting a bias toward the right side of space likely due to biomechanical constraints of the right arm (and, in addition, all participants were right-handed). See Table 2-3 for means of all kinematic measures.

2.5.2 Supplemental Experimental Procedures

Participants were comfortably seated in front of a table. A start button was located 15 cm from the edge of the table at the participant's midline and was used to measure reaction times. Located 40 cm from the start button (55 cm from participant) was a 40-in touch screen (NEC MultiSync® LCD4020), which was used to display targets on each trial. The presentation of target stimuli was controlled with custom Matlab software (version 6.5) in the Psychtoolbox [Version 2, 1, 2]. Reaching kinematics were recorded (at 150 Hz) from two infrared-emitting diode (IRED) markers placed on the index finger of the right hand (one on the tip, the other directly behind it) via an OPTOTRAK (Northern Digital Inc., Waterloo, Canada) motion-tracking system. Marker

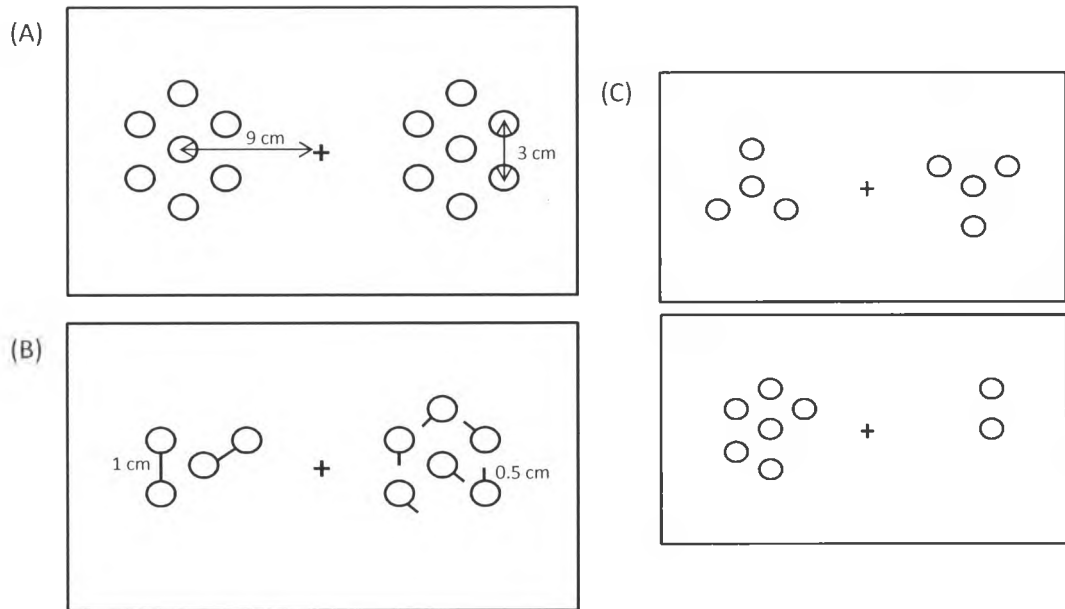
Supplemental Table 2-3. Means for kinematic measures (Reaction Time (ms), Movement Time (ms), Peak Velocity (mm/s), Time to Peak Velocity (ms), and Percent Time to Peak Velocity (%)) for both cue-sides of all trial types. Displays are not drawn to scale.

| Target on Left | | | | | Target on Right | | | | | | |
|----------------|--------|---------|--------|-------|-----------------|----|--------|--------|---------|--------|-------|
| RT | MT | PeakV | TTPV | %TTPV | RT | MT | PeakV | TTPV | %TTPV | | |
| 224.94 | 428.16 | 2373.09 | 153.75 | 36.71 | | | 227.22 | 380.18 | 2427.25 | 180.89 | 48.74 |
| 227.36 | 431.98 | 2366.70 | 155.93 | 36.84 | | | 226.64 | 374.67 | 2412.01 | 181.04 | 49.37 |
| 226.11 | 417.57 | 2315.77 | 162.41 | 39.37 | | | 224.37 | 393.88 | 2378.09 | 185.93 | 49.02 |
| 225.27 | 425.55 | 2348.92 | 155.74 | 37.31 | | | 223.89 | 380.64 | 2403.77 | 194.80 | 52.04 |
| 228.93 | 422.33 | 2355.06 | 157.42 | 37.98 | | | 228.76 | 384.26 | 2427.23 | 196.17 | 52.71 |
| 228.31 | 422.44 | 2365.26 | 169.63 | 40.73 | | | 226.00 | 380.83 | 2387.45 | 188.49 | 50.43 |
| 225.54 | 421.96 | 2323.17 | 152.35 | 36.95 | | | 224.93 | 385.75 | 2320.42 | 180.53 | 47.45 |
| 230.56 | 428.76 | 2380.39 | 161.89 | 38.69 | | | 222.88 | 384.93 | 2391.44 | 183.39 | 48.88 |
| 228.01 | 427.60 | 2354.59 | 158.77 | 38.03 | | | 221.79 | 380.10 | 2407.80 | 195.76 | 52.72 |
| 227.81 | 420.22 | 2302.72 | 165.13 | 39.97 | | | 225.58 | 389.53 | 2327.04 | 197.28 | 51.95 |
| 228.06 | 426.23 | 2365.76 | 159.57 | 38.39 | | | 223.79 | 386.73 | 2399.30 | 193.37 | 51.72 |
| 226.01 | 426.31 | 2377.78 | 153.44 | 36.54 | | | 230.43 | 373.53 | 2395.46 | 189.81 | 51.33 |
| 227.09 | 420.44 | 2374.67 | 166.64 | 40.35 | | | 225.87 | 383.58 | 2354.99 | 192.57 | 51.39 |
| 223.53 | 460.65 | 2377.42 | 148.23 | 35.07 | | | 223.54 | 380.16 | 2378.71 | 189.69 | 51.02 |
| 225.10 | 421.12 | 2349.16 | 154.41 | 37.11 | | | 228.63 | 384.86 | 2347.08 | 193.80 | 51.74 |
| 227.27 | 421.59 | 2358.82 | 157.35 | 37.94 | | | 229.11 | 376.61 | 2418.23 | 184.51 | 50.07 |
| 225.72 | 418.04 | 2306.94 | 165.38 | 39.98 | | | 225.80 | 391.24 | 2375.11 | 181.44 | 47.85 |
| 226.68 | 424.08 | 2352.98 | 154.96 | 37.69 | | | 226.24 | 385.66 | 2390.09 | 193.31 | 51.12 |
| 226.14 | 418.22 | 2384.06 | 164.06 | 40.37 | | | 229.14 | 377.05 | 2419.84 | 193.62 | 52.84 |
| 224.24 | 418.88 | 2308.28 | 162.12 | 39.33 | | | 220.94 | 394.39 | 2352.85 | 185.22 | 48.71 |
| 223.55 | 427.83 | 2369.71 | 159.15 | 37.50 | | | 228.04 | 380.79 | 2368.99 | 196.25 | 52.70 |
| 222.78 | 443.06 | 2346.81 | 158.31 | 37.71 | | | 226.97 | 386.90 | 2382.35 | 184.22 | 49.36 |
| 226.88 | 422.64 | 2338.99 | 159.14 | 38.54 | | | 227.01 | 397.71 | 2352.73 | 199.00 | 53.63 |
| 223.33 | 424.46 | 2330.74 | 153.58 | 37.05 | | | 221.67 | 385.18 | 2389.50 | 192.04 | 51.29 |
| 226.35 | 437.07 | 2394.31 | 153.08 | 36.01 | | | 227.65 | 390.69 | 2368.66 | 175.93 | 46.87 |
| 228.06 | 447.04 | 2385.18 | 162.60 | 38.58 | | | 230.44 | 373.12 | 2375.78 | 195.09 | 53.13 |
| 228.22 | 415.25 | 2364.27 | 167.42 | 40.94 | | | 226.60 | 379.91 | 2397.49 | 191.48 | 51.01 |
| 222.20 | 424.78 | 2336.50 | 165.11 | 39.32 | | | 226.35 | 383.18 | 2409.75 | 178.99 | 48.49 |

wires were held in place with a wrist band to allow for unrestricted arm movement. Three stationary IREDs were also placed on the touch screen.

The configuration of the circles in the displays was randomly chosen using a hexagon of possible locations (all locations 3 cm apart from centre to centre), with a circle in the middle of the hexagon always being chosen (centre circle of each side was 9 cm from the midline) (see Supplemental Figure 2-7). All connection (1 cm) and disconnection (0.5 cm) lines always pointed to a neighbouring circle and not outside of the hexagon shape, thus controlling for display size across the experiment. The illusion was least likely to have an effect on displays with six targets on one side and two on the other; therefore, to reduce trial number and thus experiment length these trial types were not included in the design. Additionally, particular target configurations in displays with four targets on each side of space were not included as 1-cm connection lines could not be made between neighbouring circles (see Supplemental Figure 2-7).

At the end of each trial, participants received the following visual feedback (displayed on the touch screen) indicating their performance on that trial: *Too Early* (if the start button was released before 100 ms had elapsed), *Timed Out* (if the start button was not released within 325 ms), *Too Slow* (if the response (verbal onset for perceptual task, touching the screen for reaching task) was not given within 425 ms of releasing the button), and *Good* (if the response was given in the correct amount of time (perceptual task) or if the screen was touched within a 6 cm x 6 cm box centered on the target circle (not visible to participants) within the correct amount of time (reaching task)). For the reaching task only, *Miss* was displayed if the screen was touched outside of the 6 cm x 6 cm box. Trials deemed *Too Early* or *Timed Out* were aborted and a target display did not



Supplemental Figure 2-7. (A) **Configurations:** All target configurations were created from a hexagon of equally spaced possible locations, with the centre circle always being chosen. (B) **Connection and Disconnection Lines:** Small lines connected neighbouring circles to create connected pairs; half lines extended toward neighbouring circles without ever meeting another line to create disconnected target displays. (C) **Excluded Trial Types:** Configurations for which 1-cm connections could not be made to neighbouring circles and trial types for which a comparison of the left and right sides was least likely to produce a reliable underestimation effect were excluded. Displays are not drawn to scale.

appear on the screen.

Both the perceptual and reaching tasks included a total of 28 different trial types (seven target configurations each with four levels of connectedness) for which the goal target could appear on either side of space. The perceptual task included 280 trials divided into seven blocks (40 trials/block), with ten repetitions of each trial type randomly distributed across the entire experiment. The reaching task included 680 trials divided into 17 blocks (40 trials/block), with at least ten repetitions of each trial type. Across the entire experiment, the goal target appeared an equal number of times on both sides of space to control for the effects of side bias [21].

2.5.3 Supplemental Analytical Procedures

2.5.3.1 Data Removal

For both tasks, we aborted and discarded trials where participants failed to meet the reaction time requirements ($100 \text{ ms} < \text{reaction time} < 325 \text{ ms}$). During analysis, we removed the 5% of trials with the slowest movement (reaching task) and response (perceptual task) times (across all participants) as well as all trials where participants missed the target (for the reaching task only). After removing these trials, participants were excluded if they did not have at least four repetitions of each trial type in the reaching task and/or five repetitions of each trial type in the perceptual task. Seven participants were excluded due to these criteria.

2.5.3.2 Processing of Reaching Data

All analyses were conducted on data from the IRED on the tip of the right index finger. Raw 3D data for each trial were filtered using a low-pass Butterworth filter (dual pass, 10 Hz cutoff, 2nd order). Instantaneous velocities in each cardinal dimension (x, y,

z) were calculated for each time point and the resulting velocity profiles were filtered (low-pass Butterworth filter, dual pass, 12 Hz cutoff, 2nd order) and combined to create a vector velocity (i.e. three-dimensional) profile for each trial. Onset of reaches were defined as the first of four consecutive vector velocity readings of greater than 20 mm/s where there was a total acceleration of 20 mm/s² across the four points. Reaches were said to terminate with whichever of two conditions was first met: the maximum value in the y-direction was obtained or the first time the velocity dropped below 20 mm/s.

Missing data from the index finger-tip IRED that was temporarily blocked from the view of the OPTOTRAK was filled in with translated data from the second index-finger IRED immediately behind it.

Trials were also rejected for the following reasons: the reach never attained the defined minimum velocity, the reach did not terminate within the recording window, the reach was too short in either duration (< 100 ms) or distance (< 200 mm in depth), or errors in OPTOTRAK recording (usually due to blocked IREDs) caused velocity spikes > 6000 mm/s. Under these criteria, < 1% of the trials were rejected.

All trajectories were translated such that the first reading of the index-finger-tip IRED was taken as the origin of the trajectory (i.e. 0,0,0 in 3D Cartesian space, x = horizontal, y = depth, z = vertical). They were then rotated such that the direction of movement (y) was orthogonal to the plane of the touch screen (defined by the stationary IREDs on the screen).

Spatial averaging of trajectories used functional data analysis techniques [31]. For each participant and each trial, the discrete data in the extracted reach trajectory was fit using B-splines. Spline functions are commonly used to fit motion data that are not

strictly periodic [32, 33]. For an example of recent papers using a similar technique see [34, 35]. Order 6 splines were fitted to each of the three dimensions (x, y, z) of the motion data with a spline at every data point. The data were smoothed using a roughness penalty on the fourth derivative ($\lambda = 10^{-18}$, within 0.00001 of the generalized cross-validation estimate; [31]), which allowed for control of the smoothness of the second derivative.

The result of the spline-fitting process is a functional data object for each of the three dimensions that contains a mathematical formulation of the reach. Since the trajectory was now mathematically defined, we could define the reach at any scale (i.e. with any number of points). Therefore, to average our trajectories, we evaluated each of the y (reach direction) components of the reach at 2000 equally spaced points (in time). We then extracted the location and times that corresponded to 200 points that were equally spaced along the distance of the y-trajectory. We were then able to proceed with spatial averaging that corresponded to trajectories normalized to y-distance (which was comparable for all reaches made to the touch screen which remained at a fixed distance). To do this, we evaluated both the x and z components of the reach at the newly y-normalized times then averaged across trials within the same condition for each participant, and finally across participants to produce our average trajectory plots.

2.5.3.3 *Functional Analysis*

A functional-ANOVA [31] was used to evaluate trajectory differences between all conditions of interest in the lateral (x) dimension. A functional-ANOVA is an extension of the traditional ANOVA (with only a single dependent variable across groups) to data that is continuous (like the spline-fitted trajectories in the current experiment). Therefore, where a traditional ANOVA gives a single F-statistic which indicates differences among

means, the functional-ANOVA gives a functional F-statistic which shows not only if, but where and to what magnitude a set of functionally defined measures differ across trial types. We therefore report the regions where our comparisons significantly differ by placing significance bars to the side of our trajectories that correspond to the specific comparisons being made. The intensity of the significance bar denotes the magnitude of the significant difference (as captured by the p-value of the comparison – see Figures 2-3 and 2-4, and Supplemental Figures 2-5 and 2-6).

The functional-ANOVAs used to compare the trajectories within each condition (i.e. where number of targets is fixed) were seven single-factor repeated-measures design with four levels corresponding to the four trajectories toward the different levels of connectedness. In addition, four single-factor repeated-measures functional-ANOVAs were used to compare different target-number conditions within a fixed connectedness level (e.g. compare all conditions (based on target number) when both sides were connected). A Greenhouse-Geisser correction for sphericity was applied separately for each of the 200 points evaluated. Where and to what degree this functional-ANOVA was significant is indicated with the gradient black bar in all trajectory plots. These significant bars are the result of post hoc analyses for the respective comparisons. The functional pairwise comparisons were implemented as a two-level repeated measures functional-ANOVA (equivalent to a paired t-test).

Overall, the results of our functional analysis revealed significant differences between reaches with a fixed connectedness level but differing numbers of targets. Conversely, when target number was kept constant but connectedness level was varied,

no significant differences in reach trajectories were found. Therefore, object connectedness did not influence the planning and execution of strategic reaches.

2.6 References

- [1] Goodale, M.A. & Milner, A.D. (1992). Separate visual pathways for perception and action. *Trends in Neurosciences*, 15, 20-25.
- [2] Milner, A.D., Perrett, D.I., Johnston, R.S., Benson, P.J., Jordan, T.R., Heeley, D.W., Bettucci, D., Mortara, F., Mutani, R., Terazzi, E., & Davidson, D.L.W. (1991). Perception and action in visual form agnosia. *Brain*, 114, 405-428.
- [3] Goodale, M.A., Milner, A.D., Jakobson, L.S., & Carey, D.P. (1991). A neurological dissociation between perceiving objects and grasping them. *Nature*, 349, 154-156.
- [4] Cohen, Y.E., & Andersen, R.A. (2002). A common reference frame for movement plans in the posterior parietal cortex. *Nature Review in Neuroscience*, 3, 553-562.
- [5] Culham, J.C., Danckert, S.L., SeSouza, J.F.X., Gati, J.S., Menon, R.S., & Goodale, M.A. (2003). Visually guided grasping produces fMRI activation in dorsal but not ventral stream brain areas. *Experimental Brain Research*, 153, 180-189.
- [6] Shmuelof, L., & Zohary, E. (2005). Dissociation between ventral and dorsal fMRI activation during object and action recognition. *Neuron*, 47, 457-470.
- [7] Goodale, M.A., Gonzalez, C.L.R., & Króliczak, G. (2008). Action rules: Why the visual control of reaching and grasping is not always influenced by perceptual illusions. *Perception*, 37, 355-366.
- [8] Goodale, M.A. (2010). Transforming vision into action. Vision Research. doi:10.1016/j.visres.2010.07.027
- [9] Westwood, D.A., & Goodale, M.A. (2010). Converging evidence for diverging pathways: Neuropsychology and psychophysics tell the same story. Vision Research. doi:10.1016/j.visres.2010.10.014
- [10] Króliczak, G., Heard, P., Goodale, M.A., & Gregory, R.L. (2006). Dissociation of perception and action unmasked by the hollow-face illusion. *Brain Research*, 1080, 9-16.
- [11] Franconeri, S.L., Bemis, D.K., & Alvarez, G.A. (2009). Number estimation relies on a set of segmented objects. *Cognition*, 113, 1-13.
- [12] He, L., Zhang, J., Zhou, T., & Chen, L. (2009). Connectedness affects dot numerosity judgment: Implications for configural processing. *Psychonomic Bulletin & Review*, 16, 509-517.
- [13] Westheimer, G. (1999). Gestalt theory reconfigured: Max Wertheimer's anticipation of recent developments in visual neuroscience. *Perception*, 28, 5-15.

- [14] Wise, S.P., Boussaoud, D., Johnson, P.B., & Caminiti, R. (1997). Premotor and parietal cortex: Corticocortical connectivity and combinatorial computations. *Annual Reviews in Neuroscience*, 20, 25-42.
- [15] Cisek, P., & Kalaska, J.F. (2005). Neural correlates of reaching decisions in dorsal premotor cortex: Specification of multiple direction choices and final selection of action. *Neuron*, 3, 801-814.
- [16] Cisek, P., & Kalaska, J. F. (2002). Simultaneous encoding of multiple potential reach directions in dorsal premotor cortex. *Journal of Neurophysiology*, 87, 1149-1154.
- [17] Song, J.H., & Nakayama, K. (2008). Target selection in visual search as revealed by movement trajectories. *Vision Research*, 48, 853-861.
- [18] Song, J.H., & Nakayama, K. (2009). Hidden cognitive states revealed in choice reaching tasks. *Trends in Cognitive Science*, 13, 360-366.
- [19] Chapman, C.S., Gallivan, J.P., Wood, D.K., Milne, J.L., Culham, J.C., & Goodale, M.A. (2010). Reaching for the unknown: Multiple target encoding and real-time decision-making in a rapid reach task. *Cognition*, 116, 168-176.
- [20] Oldfield, R.C. (1971). The assessment and analysis of handedness: The Edinburgh inventory. *Neuropsychologia*, 9, 94-113.
- [21] Chapman, C.S., Gallivan, J.P., Wood, D.K., Milne, J.L., Culham, J.C., & Goodale, M.A. (2010). Short-term motor plasticity revealed in a visuomotor decision-making task. *Behavioural Brain Research*, 214, 130-134.
- [22] Kaufman, E.L., Lord, M.W., Reese, T., & Volkman, J. (1949). The discrimination of visual number. *American Journal of Psychology*, 62, 496-525.
- [23] Trick, L.M., & Pylyshyn, Z.W. (1994). Why are small and large numbers enumerated differently? A limited-capacity pre-attentive stage in vision. *Psychological Review*, 101, 80-102.
- [24] Burr, D.C., Turi, M., & Anobile, G. (2010). Subitizing but not estimation of numerosity requires attentional resources. *Journal of Vision*, 10, 1-10.
- [25] Vetter, P., Butterworth, B., & Bahrami, B. (2008). Modulating attentional load affects numerosity estimation: Evidence against a pre-attentive subitizing mechanism. *PLoS ONE*, 3, e3269.
- [26] Glover, S., Rosenbaum, D.A., Graham, J., & Dixon, P. (2004). Grasping the meaning of words. *Experimental Brain Research*, 154, 103-108.

- [27] Mendoza, J., Hansen, S., Glazebrook, C.M., Keetch, K.M., & Elliot, D. (2005). Visual illusions affect both movement planning and on-line control: A multiple cue position on bias and goal-directed action. 2005. *Human Movement Science*, 24, 760-773.
- [28] Goodale, M.A., & Westwood, D.A. (2004). An evolving view of duplex vision: Separate but interacting cortical pathways for perception and action. *Current Opinion in Neurobiology*, 14, 203-211.
- [29] Franz, V.H., Gegenfurtner, K.R., Bühlhoff, H.H., & Fahle, M. (2000). Grasping visual illusions: No evidence for a dissociation between perception and action. *Psychological Science*, 11, 20-25.
- [30] Paulignan, Y., Jeannerod, M., MacKenzie, C., & Marteniuk, R. (1991). Selective perturbation of visual input during prehension movements. II. The effects of changing object size. *Experimental Brain Research*, 87, 407-420.
- [31] Ramsay, J.O., & Silverman, B.W. (2005). *Functional data analysis*, 2nd Edition. New York: Springer.
- [32] Ramsay, J.O. (2000). Functional components of variation in handwriting. *Journal of the American Statistical Association*, 95, 9-15.
- [33] Ramsay, J.O., Munhall, K.G., Gracco, V.L., & Ostry, D.J. (1996). Functional data analyses of lip motion. *Journal of the Acoustical Society of America*, 99, 3718-3727.
- [34] Loehr, J.D., & Palmer, C. (2005). Cognitive and biomechanical influences in pianists' finger tapping. *Experimental Brain Research*, 178, 518-528.
- [35] Loehr, J.D., & Palmer, C. (2009). Sequential and biomechanical factors constrain timing and motion in tapping. *Journal of Motor Behavior*, 41, 128-136.

Chapter 3

General Discussion

3.1 General Discussion

3.1.1 Summary of Findings

The aim of the current experiments was to determine if visual action and perception could be behaviourally dissociated using a perceptual illusion. Specifically, we applied an illusion in which connected objects (for example, two circles connected by a single line) appear as one and thus result in the underestimation of the total number of objects in a set. Using a unique paradigm we developed to test for multiple object encoding, participants made speeded reaches toward target displays in which a goal location is not specified until after movement onset. Unlike typical tasks that use discrete measures such as reaction times and peak grip apertures, we were able to represent reach trajectories in a continuous fashion, and through the use of sophisticated analyses we could determine how the movements unfolded over time. While we found a clear and robust effect of object connectedness on perception, there was no evidence of an effect of the illusion on the rapid reaches.

Specifically, we were able to replicate our previous work and show that participants planned and executed reaches based on the spatial distribution of potential targets. That is, reaches extended toward an averaged spatial location and therefore maximized chances of success when the goal target was cued. Critically, the presence of connected pairs in the target displays did not disrupt this strategic behaviour; the visuomotor system was able to ignore the connections and instead plan reaches based on the veridical number of targets. For example, in cases where target distribution was equal (for example, two targets on each side of space), the presence of connections in either the left or right side did not bias trajectories in the opposite direction, despite participants

judging the side with connections as containing fewer objects in the perceptual task. The lack of an effect of the illusion on action was consistent across all trial types, and all differences that were found were based purely on changes to the number and spatial distribution of the targets.

3.1.2 Relation to Existing Literature

Our results are consistent with much of the research in this area: that rapid, automatic actions are resistant to the effects of perceptual illusions [e.g. 1-3]. Specifically, we found that an illusion with Gestalt properties was unable to permeate the planning of strategic reaches. Interestingly, though, some of our most recent work has suggested that changes in saliency due to manipulations of continuity (another Gestalt property) can influence the reaching behaviour seen in our task (unless given additional processing time to overcome the effects of saliency features) [in preparation]. While these differences may seem puzzling, it is likely due to how the features affect the processing of the targets themselves. For example, changes in saliency directly influence the characteristics of the actual targets, whereas connectedness did not define the targets but rather had the potential to influence the enumeration of the total number in the displays. It seems likely, then, that this crucial difference accounts for why the Gestalt illusion used in the current work did not affect movement planning or execution, even without additional processing time.

While there is a breadth of research supporting a behavioural dissociation between perception and action, these claims do not come without criticism. With the unique representation and analysis used in the current work, however, we are able to directly address some of the existing criticisms. For example, in applying the Ebbinghaus

illusion to action tasks, it has been argued that the annulus of circles surrounding the target disk may act as an obstacle and therefore disrupt the programming of the movement [for example, see 4]. One could argue that in our task there are numerous obstacles and that this could account for the deviations in reaches that we see. This is not a valid argument, however, because when participants initiate their movements all targets serve as potential goals, not as distractors or obstacles. It is only when the goal target is cued that all remaining targets become distractors. At that point, however, we were already able to see that the initial phase of the movement was not influenced by the illusion.

In addition to a dissociation of action and perception, our results support our original claims and suggest that each individual target was being encoded for action [5, 6], which is consistent with neurophysiological findings in monkeys [7, 8]. While most previous studies have required participants to focus on a single goal, we were able to show that, even in the presence of multiple goals, rapid action is able to overcome the presence of a perceptual illusion and strategic movements that account for multiple goals can be accurately planned and executed. Our results, then, not only support the two visual streams account, but also support a parallel encoding view that suggests multiple objects can be prepared for action simultaneously.

3.1.3 Future Directions

An important motivating factor for the current work was to determine how much the behaviour seen with our paradigm relies on dorsal and/or ventral processes. While our findings certainly suggest the strategic actions are heavily dorsally-mediated (presumably via links to premotor cortex), it will be important to extend our work to brain-damaged

populations to gain a better understanding of the neural substrates of the behaviour.

Particularly, patients with localized lesions specific to the ventral and dorsal streams (and other related brain areas, including premotor cortex) will help us to pinpoint the processing that underlies this spatial averaging behaviour. Additionally, transcranial magnetic stimulation will be useful in investigating the effects of temporary virtual lesions to, for example, the dorsolateral prefrontal cortex or intraparietal sulcus in healthy populations. Overall, our aim will be to continue using our powerful and versatile paradigm to further understand visually-guided action toward multiple goals.

3.1.4 Conclusions

While it is likely that perception developed to allow for complex operations on representations of the world – including aiding in flexible and adaptive behaviour – it is clear that the visuomotor system is still able to function in a rapid and automatic fashion that is independent from the richer and more sophisticated processes of the ventral stream. The current work provides compelling evidence for a dissociation of perception and action and adds to the existing literature as it shows the dissociation even in the presence of multiple goals. In addition, our work directly addressed common criticisms in the action-perception literature through our unique paradigm and sophisticated trajectory analysis. Future work should aim to further understand the processes underlying the unique behaviour seen in our paradigm to ultimately come to a better understanding of visually-guided actions toward multiple goals.

3.2 References

- [1] Haffenden, A.M., & Goodale, M.A. (1998). The effect of pictorial illusions on prehension and perception. *Journal of Cognitive Neuroscience*, *10*, 122-136.
- [2] Króliczak, G., Heard, P., Goodale, M.A., & Gregory, R.L. (2006). Dissociation of perception and action unmasked by the hollow-face illusion. *Brain Research*, *1080*, 9-16.
- [3] Dewar, M.T., & Carey, D.P. (2006). Visuomotor 'immunity' to perceptual illusion: A mismatch of attentional demands cannot explain the perception-action dissociation. *Neuropsychologia*, *44*, 1501-1508.
- [4] Haffenden, A.M., & Goodale, M.A. (2000). Independent effects of pictorial displays on perception and action. *Vision Research*, *40*, 1597-1607.
- [5] Chapman, C.S., Gallivan, J.P., Wood, D.K., Milne, J.L., Culham, J.C., & Goodale, M.A. (2010). Reaching for the unknown: Multiple target encoding and real-time decision-making in a rapid reach task. *Cognition*, *116*, 168-176.
- [6] Chapman, C.S., Gallivan, J.P., Wood, D.K., Milne, J.L., Culham, J.C., & Goodale, M.A. (2010). Short-term motor plasticity revealed in a visuomotor decision-making task. *Behavioural Brain Research*, *214*, 130-134.
- [7] Cisek, P., & Kalaska, J.F. (2005). Neural correlates of reaching decisions in dorsal premotor cortex: Specification of multiple direction choices and final selection of action. *Neuron*, *3*, 801-814.
- [8] Cisek, P., & Kalaska, J. F. (2002). Simultaneous encoding of multiple potential reach directions in dorsal premotor cortex. *Journal of Neurophysiology*, *87*, 1149-1154.