Response competition operates on movement direction and is effector-independent: Evidence from three free choice reaching tasks

by

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

Master of Science

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Abstract

People and other organisms live in complex environments where the number of potential actions is almost always greater than the number of actions that can be performed at a time. Thus, organisms must make decisions about which actions to perform and which to not perform. Theories about how action decisions occur fall into two broad categories: serial and parallel. Serial theories claim that a decision about which action to perform is made before the movements required to complete the action are specified; thus, only one action is ever planned at a time. In contrast, parallel theories claim that movements can be specified prior to such a decision, resulting in two or more potential actions being planned simultaneously. The affordance competition hypothesis, proposed by Paul Cisek in 2007, is a parallel theory which claims that actions are decided upon via competitive process between movement plans. The novelty of this hypothesis is that it proposes a starring role for the “motor” system in the decision-making process, eliminating the need for any sort of dedicated “decision system”. According to Cisek, movement planning is not the outcome of decision-making, but is instead the basis for it. Most of the experiments designed to test this hypothesis, however, involve cued actions rather than actions which are chosen endogenously by the participant. Cued actions are comparatively rare outside of lab conditions, with the majority of actions performed voluntarily according to an individual’s internal motives. In this thesis, I report three experiments which were intended to test the affordance competition hypothesis under the more ecologically relevant condition of allowing participants to choose their actions rather than having actions chosen for them. Experiment 1 established the basic procedure of the thesis project, with participants being presented with a small, circular target in one of several possible lateralized locations, then given the choice of reaching out and touching the target with either their left hand or their right hand. In this experiment, participants responded more slowly to targets near the center of the screen, where the likelihood of using each hand was roughly equal, than they did to more lateralized targets where one hand performed the vast majority of responses. In Experiment 2, each target was preceded by a fixation cross in one of two possible lateralized locations. This arrangement required participants to perform both eye and hand movements to each target without making those movement directions necessarily congruent. Participants responded faster during trials where the eye and hand movements were congruent versus incongruent trials. In Experiment 3, a cue condition was added in order to explicitly contrast the results of Experiments 1 and 2 against results obtained under this more common experimental condition. Unlike voluntary actions, which were slower to central targets just as they were in Experiment 1, cued actions were actually performed faster to central targets, and were also performed more accurately overall. In line with the affordance competition hypothesis, the results of these three experiments suggest that people engage in a process of movement competition based on movement direction during voluntary actions. The results also suggest that voluntary and cued actions exhibit unique neurological and kinematic characteristics.

Preface

This thesis is an original work by Alice Elizabeth Atkin, under the supervision of Dr. Anthony Singhal. Data for this thesis was collected with the approval of the University of Alberta Research Ethics Board, project number 1785 (CDH08-514).

All three experiments presented in this thesis were designed by Alice Atkin and Dr. Anthony Singhal. Data was collected by Alice Atkin and Sayeed Devraj-Kizuk, and was analyzed by Alice Atkin.

Dedicated to my parents

Acknowledgements

My ability to start and finish this thesis owes itself to a great many people and I will certainly get to everyone, but there’s no other way I can start this section than by thanking my supervisor, Anthony Singhal. Thank you so, so much for accepting me as your student (twice!). Thank you for your time. Thank you for your knowledge. Thank you for your wisdom. But most of all, thank you for your kindness. I will never forget all that you have done for me.

Thank you as well to the current and former Singhal Lab students and postdocs who encouraged this thesis and made (almost) every day in the lab enjoyable and interesting: Graeme Armstrong, Michelle Chan, Yvonne Chen, Leanna Cruickshank, Sarah Elke, Chris Madan, Andrea Schafer, Ian Surdhar, and Yvonne Wong. I would like to offer a special thank you to Michelle, Leanna, and Ian, whose experience and knowledge in performing combined behavioural-EEG experiments made the first year of my program as easy as any first year can be. Thank you as well to Sayeed Devraj-Kizuk and every other current and former Singhal Lab undergraduate research assistant for your assistance and enthusiasm.

Thank you to Peter Dixon, Sandra Wiebe, and Clayton Dickson, for serving on my supervisory committee and for doing their very best to keep my graduate program moving (I’m so sorry it’s taken me this long to get here!). Thank you to Craig Chapman for your insightful and supportive comments about my work and my ideas. Thank you to Anita Mueller, Jan Boulter, and the entire Department of Psychology office for your years of administrative assistance.

Thank you to all my friends, who have seen the worst of me and the best of me and loved me all the same. I've been to your birthdays, your thesis defenses, your weddings and your parties, and I'm so pleased to be able to share this happy moment of my own with you just as you have shared yours with me.

Thank you to my grandmother Elizabeth and my grandfather Ralph. From childhood trips to the beach to look for interesting things to the money you still slip into my hand every time I leave your house, "for sweets", you've taught me appreciate life's smallest pleasures. I promise I always will.

And, finally, the most profound thank you of all to my Dad, Arnie, and my Mum, Helen. If I'd begun this acknowledgement section with you there would have been no words left for anybody else. No part of this thesis would have been possible without your unwavering love and support. You're the best parents I could have ever asked for, and I love you so very much.

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1 – Introduction

The affordance competition hypothesis (Cisek, 2006, 2007; Cisek & Kalaska, 2005) is a hypothesis about visuomotor behaviour which claims that organisms prepare multiple potential actions simultaneously before deciding between them. The hypothesis reverses the widely-held information-processing model of visuomotor behaviour, which claims that organisms decide upon an action before preparing and executing that action. In order to explain the hypothesis more fully, and to justify the three tests of the hypothesis that this thesis presents, it will be necessary to describe the research which led to the formulation of the hypothesis, as well as the nature of affordances. Aspects of the experiments reported in this thesis which are relevant to the experiments without being fundamental to the hypothesis itself, such as volition, motor perseveration and visual reference frames, will also be touched upon.

1.1 – Affordances

Introduced into the psychological vocabulary by J.J. Gibson (1977, 1979/2014), affordances are, generally speaking, opportunities for action. To Gibson, affordances were much more than opportunities for action, though; they were the fundamental units of perception. An in-depth recounting of Gibsonian metaphysics is unnecessary for our purposes, however, because the concept of an opportunity for action is useful whether or not one agrees with Gibson about the nature and importance of affordances to organisms. All that matters is that it is somehow possible for organisms to act in a variety of ways, and for organisms to determine through perception which actions are appropriate and inappropriate at a particular place and time.

Do organisms act in a variety of ways? The answer, obviously, is yes. Humans alone are capable of grasping, pointing, lifting, pushing, pulling, walking, running, jumping, swimming, climbing, throwing, and a nearly uncountable number of other actions. Many of these actions are capable of being performed simultaneously; I can throw a baseball while running, I can reach for and grasp a teacup with one hand while reaching for and grasping a pencil with the other, etc. Many actions cannot be performed simultaneously, however. Limb movement is a vector, meaning that movements towards one direction are necessarily movements away from the other; I cannot reach for a teacup and a pencil with the same hand at the same time. In this and in many other situations, decisions must be made about which action to perform and which actions to forgo.

Can organisms determine which actions are appropriate by perceiving their environment? Again, the answer is clearly yes. In fact, there is substantial evidence that the presence of interactive objects automatically evokes appropriate motor activity even when the task does not require it (Bub & Masson, 2010; Ellis & Tucker, 2000; Handy et al., 2003; Phillips & Ward, 2002; Tipper et al. 2006; Tucker & Ellis, 1998, 2001). Elaborating on this finding, two experiments by Masson et al. (2011) demonstrate that automatic motor activation is sensitive to higher-level activity relating to experience, with objects in canonical orientations evoking greater activity than objects in non-canonical orientations (Figure 1.1). In the first experiment, participants were shown a prime image of a beer mug or a frying pan in an upright or horizontal orientation. Participants were then shown an image of a hand performing either an upright or horizontal grasp and asked to mimic the grasp on a handle-shaped apparatus. The type of grasp that participants performed in response to the hand image could therefore be congruent or incongruent with the type of grasp afforded by the preceding prime. Beer mugs and frying pans were chosen because they respectively afford upright and horizontal grasps in their normal orientation, and it is worth noting that the prime did not predict the type of grasp to be performed. In line with prior experiments, the results showed a significant effect of congruency on response time: presenting an image of a graspable object resulted in faster grasping performance on a subsequent task when the two grasps were congruent, even though the prime is actually irrelevant to the task. In a subsequent experiment, the prime images were mirrored such that actually grasping a real-life version of the object in that orientation would not permit functional use (for example, it would result in holding a beer mug upside-down, thus spilling its contents). In contrast to the first experiment, an interaction between congruency and rotation was found instead: the rotated primes no longer facilitated congruent grasps. Together, these two experiments demonstrate that affordances do not arise in the mere presence of graspable objects, but instead take into account the ability to functionally use those objects.

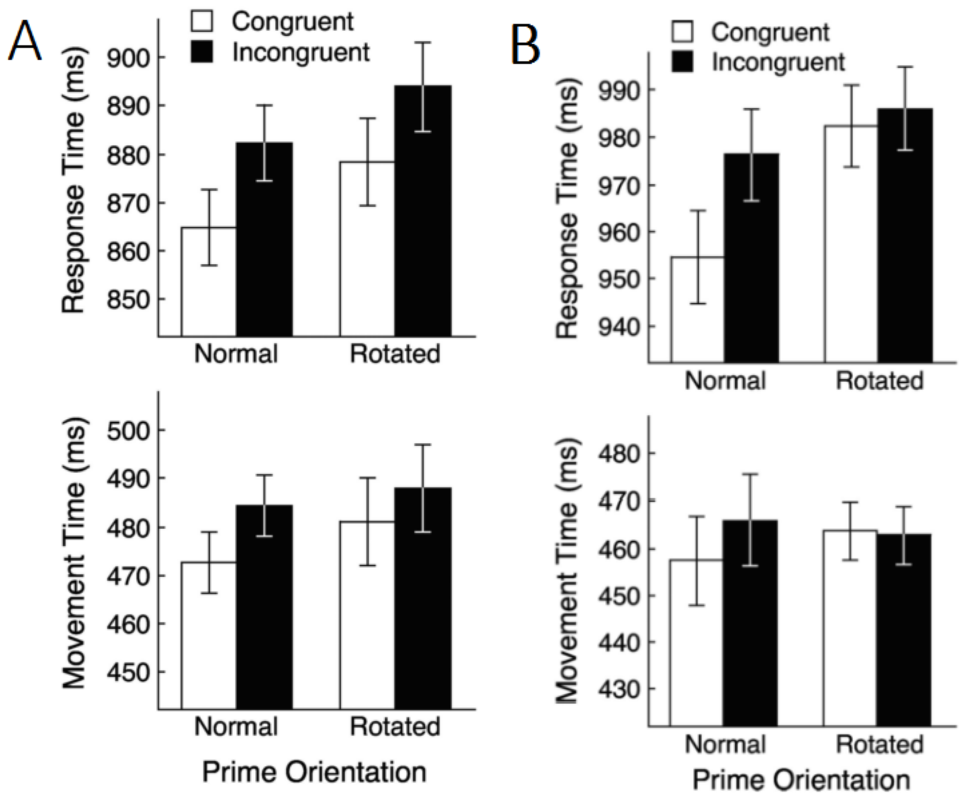

Figure 1.1 – The result of two experiments by Masson et al. (2011). **A.** Results from the first experiment, showing a main effect of grasp congruency on response time. Presenting images which afforded a particular grasp automatically evoked relevant motor planning, resulting in faster performance on an unrelated grasping task. Such affordances arise regardless of whether the object is displayed in it's normal orientation or in a rotated orientation. **B.** Results from a subsequent experiment with mirrored primes, showing that image primes afford congruent grasps when performance would result in functional use of the object (Normal), but not when performance would result in non-functional use (Rotated). Affordances reflect the potential usability of objects, not just their mere presence. Reprinted from Masson et al. (2011). Priming of reach and grasp actions by handled objects. Journal of Experimental Psychology: Human Perception and Performance, 37(5), 1470-1484. Copyright 2011, American Psychological Association.

The higher-level nature of affordances may not seem especially surprising, particularly with respect to manufactured objects, given that the ability to interact with such objects often requires learning how to use them. Turner (2005) offers the example of a tourist in Britain being unable to leave a train carriage because she could not find the interior door handle, not knowing that such doors only have exterior handles which must be reached for through a window (Figure

1.2); in my home city of Vancouver, some city buses have electronically-operated doors which require pressing a touch-sensitive strip, and I too have seen many riders search the door in vain for something resembling a physical handle or push-bar.

Figure 1.2 – An example of a door with an exterior handle. The means of opening the door is not perceptible to passengers inside the train, meaning that only passengers with prior knowledge of the handle's location can successfully open it. In Gibson's terminology, the door does not afford opening to passengers inside the train. An affordance is an opportunity for action; without an affordance, novice train passengers and bus riders typically stand helplessly at the door until somebody else comes to their rescue. Reprinted from Turner, P. (2005). Affordance as context. Interacting with Computers, 17(6), 787-800. Copyright 2005, Elsevier B.V.

To summarize, affordances are opportunities for action which are perceived by organisms with the capability to perform those actions (for more formal takes on affordances than I have provided, see Chemero, 2003, 2009; Millikan, 2000; Reed, 1996; Sahin et al., 2007; Stoffregen, 2000; 2003; Turvey, 1992; and Turvey et al., 1981). Given the requisite experience, affordances will be perceived automatically and boost the performance of concurrent tasks which make use of overlapping neural resources. Since many actions cannot be performed simultaneously, organisms frequently perceive more affordances than they can act upon at any given moment. Thus, organisms must make choices about which affordances they should act upon. For visually-guided actions, the part of the cortex that performs these decisions is the dorsal stream.

1.2 – The Dorsal Stream

In humans and other organisms with a cortex, cortical vision appears to be bifurcated into two streams of processing. This is the two-streams hypothesis, first proposed by Mishkin and Ungerleider (1982; Mishkin et al., 1983) then revised by Goodale and Milner (1992; Goodale et al. 1994; 2004; Milner & Goodale, 1993, 2006, 2008). The two-streams hypothesis claims that visual information projects along two pathways from the occipital cortex. One, the ventral stream, projects to the inferotemporal cortex, while the other, the dorsal stream, projects to the posterior parietal cortex (PPC). The apparent function of the ventral stream is to identify features of the environment, with separate substreams for the detection of colour, shape, and motion (Felleman & Van Essen, 1991; Zeki, 1980). The apparent function of the dorsal stream, meanwhile, is to enable visually guided actions. Damage to these two systems produces distinct syndromes; damage to the ventral stream results in visual agnosia, the impaired inability to identify objects (Carey et al., 1996; James et al., 2003; Milner et al., 1991; Rubens & Benson, 1971), while damage to the dorsal stream results in optic ataxia, the impaired inability to skilfully reach for objects (Jakobson et al., 1991; Perenin & Vighetto, 1988; Pisella et al., 2000).

Experiments since the 1990's have shown that the dorsal stream is extremely extensive, projecting far beyond the PPC to the premotor cortex, the prefrontal cortex, and the basal ganglia, that the dorsal stream itself contains substreams (Binkofski & Buxbaum, 2013; Daprati & Sirigu, 2006; Rizzolatti & Matelli, 2003), and that the dorsal and ventral streams interact significantly (Heilman & Watson, 2008; Milner, 2017; Ramayya et al., 2010; Singhal et al. 2007; 2013). For example, fMRI evidence indicates that the dorsal stream performs delayed actions (where the target is no longer visible) by recruiting visual target information stored within the ventral stream and early visual areas (Singhal et al., 2013). However, the basic function of the dorsal stream in supporting visually guided actions remains supported (Goodale, 2014).

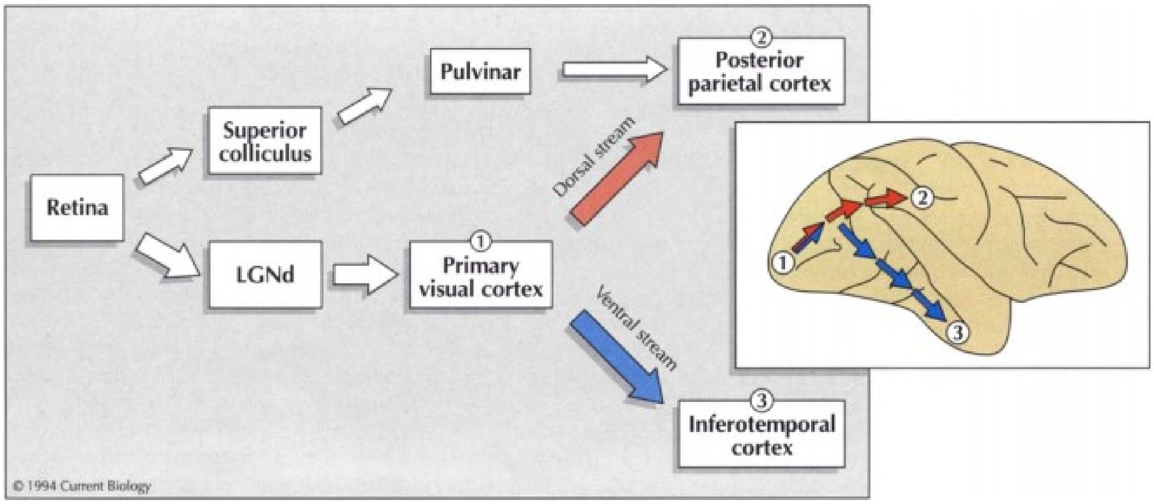

Figure 1.3 – A very basic schematic of the two-streams hypothesis as originally formulated by Mel Goodale (Goodale et al., 1994). Subsequent research has revealed that the dorsal stream contains subdivisions, and that the two streams interact significantly. Reprinted from Goodale et al. (1994). Separate neural pathways for the visual analysis of object shape in perception and prehension. Current Biology, 4(7), 604-610. Copyright 1994, Current Biology.

1.3 – Receptive Fields and Tuning Functions

A striking fact about neurons is that they display preferences. A neuron’s receptive field is the location in space where a stimulus must appear (if it’s a sensory neuron) or the location in space to which an action must be directed (if it’s a motor neuron) in order for the neuron to fire. These neurons display a characteristic bell-shaped response curve, called a tuning curve (Figure 1.4), which describes the neuron’s firing rate as a function of the property it’s tuned to (Hubel & Wiesel, 1962, 1968; Perrett et al., 1987). Neuronal tuning curves are not fixed, and can be modified by the development of the organism (Hirsch & Spinelli, 1970, 1971) and the surrounding context (Gilbert & Weisel, 1990). Neurons contributing to other sensory modalities, such as somatosensory neurons, also have receptive fields and tuning curves (Mountcastle et al., 1969; Hyvarinen & Poranen, 1978), as do motor neurons. Motor neurons in the motor cortex, for example, might fire maximally when movements are being prepared towards the left of the organism (Figure 1.4), and decrease firing when movement rotates towards the right (Georgopoulos et al., 1982; Kalaska, 1991). Receptive fields and tuning curves are such a widespread neural phenomenon that some researchers, such as Shimon Edelman (2008), claim that all cortical neurons have them.

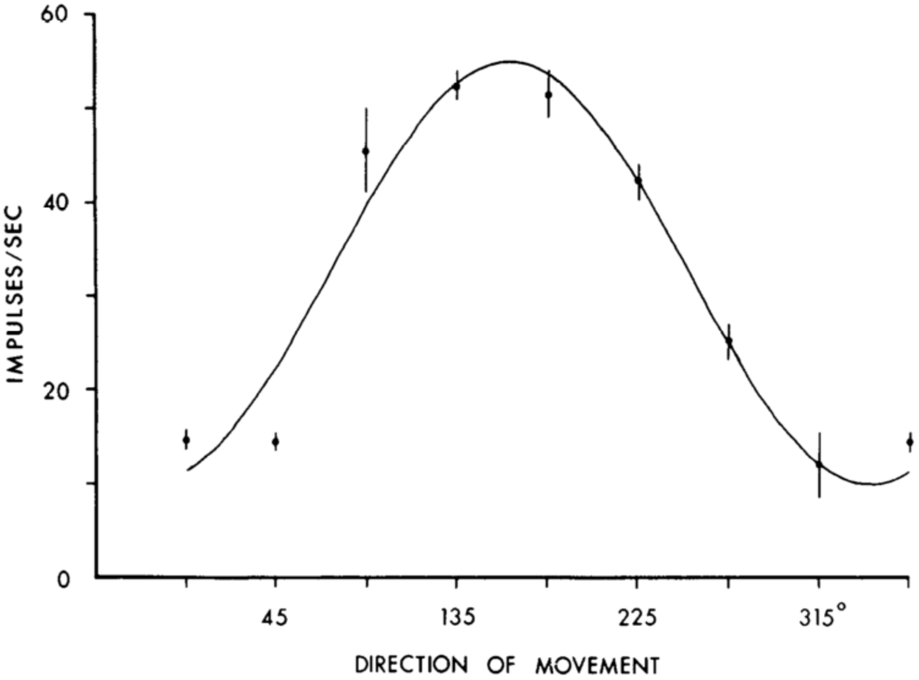

Figure 1.4 – An example of a typical tuning curve, measured from a neuron in the motor cortex of a rhesus monkey (Georgopoulos et al., 1982). The monkey performed arm movements to eight different targets arranged in a circle around the arm's starting point, with 45° of arc between each target. A movement of 0° represents a movement to the right, with degrees increasing counterclockwise. Each individual data point represents the average firing rate of the neuron during movements to each target. The firing rate of this neuron is greatest when the monkey makes arm movements to the left, with the firing rate decreasing sinusoidally with distance. Reprinted from Georgopoulos et al. (1982). On the relations between the direction of two-dimensional arm movements and cell discharge in primate motor cortex. *The Journal of Neuroscience, 2*(11), 1527-1537. Copyright 1982, Society for Neuroscience.

In recent years, tuned motor neurons have begun receiving special attention from neuroscientists because some of these neurons appear to be active both before and during movement onset (Bastian et al. 2003; Crammond & Kalaska, 1996; Georgopoulos et al., 1989). A paradigmatic example of these experiments is that conducted by Cisek & Kalaska (2002), who presented a monkey with two potential reach directions followed by a colour cue indicating the correct movement. During the delay period between the presentation of the reach directions and the presentation of the colour cue, they found that neurons tuned to the two target directions within the monkey’s dorsal premotor cortex were simultaneously active. Once the colour cue was presented, however, the non-target neurons ceased their activity. This result demonstrates that neurons tuned to different movement parameters can be active simultaneously prior to movement. In other words, organisms are capable of simultaneously preparing two movements even though it will not be possible to execute them both. This result forms the basis of the affordance competition hypothesis.

1.4 – The Affordance Competition Hypothesis

Having reviewed affordances, receptive fields, and the dorsal stream, we are now in a position to describe the affordance competition hypothesis as proposed in Cisek (2007) and review the evidence in its favour (for additional reviews, see Cisek & Kalaska, 2010; and Pezzulo & Cisek, 2016). The central claim of the affordance competition hypothesis is that organisms simultaneously prepare multiple potential movements in response to the presence of affordances, or targets of action. This occurs because neurons tuned to specific movement parameters in the dorsal stream activate automatically whenever there are potential targets which fulfill those parameters. The hypothesis is notable because it erases the traditional distinction between decision making processes and motor processes. According to the hypothesis, action selection is not a discrete cognitive system which imposes its outcomes upon the motor system, but a process which emerges organically from the interaction of motor-related neurons tuned to specific, movement parameters. A “decision system” is not necessary because the neurons which specify action are also capable of selecting it.

The benefits of this kind of parallel neural organization are numerous. By creating programs for movements to every potential target in an environment, organisms are capable of preparing (Cisek & Kalaska, 2002, 2005; Coallier et al., 2015) and even of executing movements when the target is uncertain (Chapman et al., 2010), thus permitting faster behaviour when the target becomes known than would otherwise be possible. Parallel motor plans are also capable of co-optimization, in which common movement features between plans rapidly resolve uncertain decisions, such as whether to pronate or supinate the wrist when grasping (Gallivan et al., 2015, 2016).

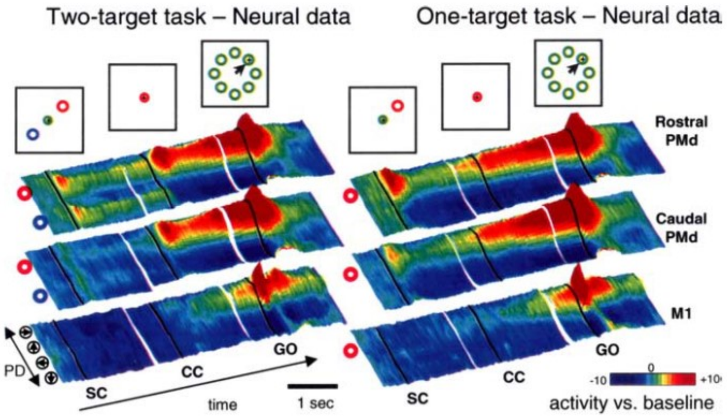

Figure 1.5 – Results from an experiment by Cisek (2005). Tuned neurons were identified within the rostral premotor cortex (rostral PMd), caudal premotor cortex (caudal PMd), and the primary motor cortex (M1) of monkeys. The monkeys were presented with one or two potential reach targets (SC). After an initial delay, the true target was cued (CC), and then after a second delay the monkeys were cued to reach to the target (GO). Results showed that during the two-target task, rostral PMd neurons tuned to either direction were simultaneously active between SC and CC, when the target identity was unknown. The ability to simultaneously prepare responses to multiple targets forms the basis of the affordance competition hypothesis. Reprinted from Cisek (2006). Integrated neural processes for defining potential actions and deciding between them: A computational model. *The Journal of Neuroscience, 26*(38), 9761-9770. Copyright 2006, Society for Neuroscience.

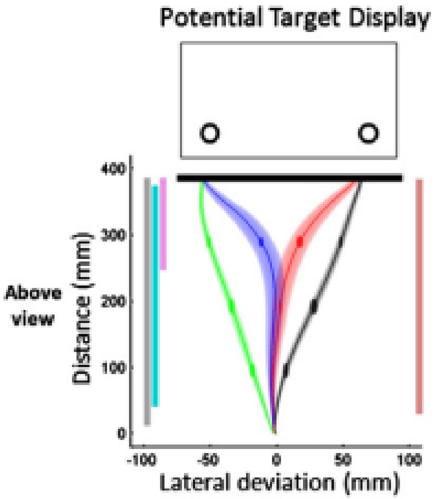

Figure 1.6 – Results from an experiment by Chapman et al. (2010). Participants were presented with one or two potential targets, but the identity of the target was not revealed until after participants began reaching. During one target trials, participants reached directly for the target (green and black tracks). During two-target trials, however, participants reached for a midpoint between the targets, only modifying their reach direction once the true target was revealed to them (blue and red tracks). This experiment demonstrates that the motor system is capable of accounting for multiple potential reach directions from planning all the way through to execution. Reprinted from Chapman et al. (2010). Reaching for the unknown: Multiple target encoding and real-time decision-making in a rapid reach task. *Cognition, 116*(2), 168-176. Copyright 2010, Elsevier B.V.

Since being proposed, several researchers have attempted to perform explicit tests of the affordance competition hypothesis. Gallivan et al. (2015) attempted to demonstrate the existence of multiple plans by presenting participants with two potential grasping targets in the shape of a rectangle, one of which was oriented so that it could be grasped via wrist pronation or via wrist supination, but not both, while the other was oriented so that it could be grasped comfortably via either method. They predicted that if parallel motor plans were being prepared for each target, then participants would be much more likely to grasp an ambiguous target with the grasp specified by the accompanying non-ambiguous non-target, and this is exactly what they found (Figure 1.6). Response times were also faster when participants performed the grasp specified by the nontarget than when they performed the opposite grasp (Figure 1.6). In a modification of that experiment, Gallivan et al. (2016) also found that participants were more likely to grasp ambiguous targets with such "co-optimized grasps" even if the targets are presented in sequence, rather than simultaneously (Figure 1.7). Interestingly, this co-optimization was bi-directional: the presentation of a non-ambiguous nontarget prompted participants to preferentially perform the co-optimized grasp regardless of whether the nontarget was presented first or second. This modified experiment not only reinforces the previous finding that parallel motor plans are automatically created in the presence of multiple potential targets, it also indicates that these plans are online and dynamic, and therefore capable of facilitating behaviour within a rapidly-changing ecological environment.

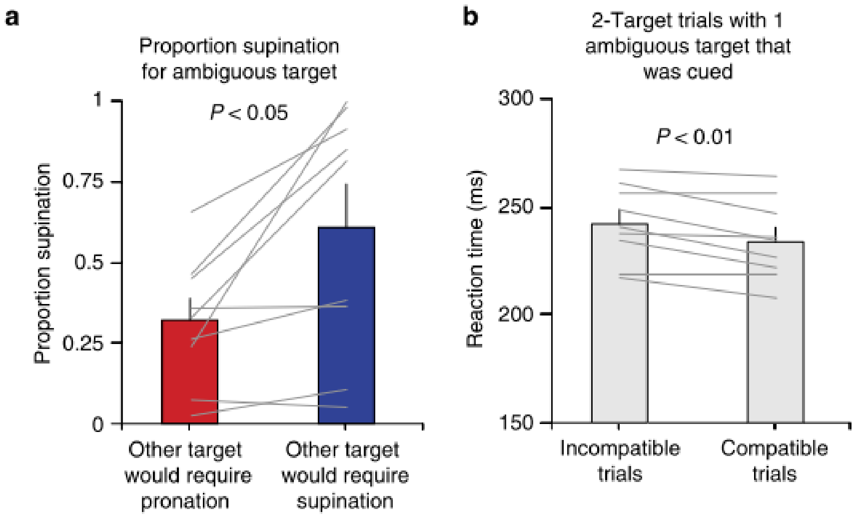

Figure 1.7 – Results from Gallivan et al. (2015). **A.** Participants were significantly more likely to supinate towards an ambiguous target when it was accompanied by a nontarget that required supination versus a nontarget that required pronation. Bar graphs represent participant grand averages and lines represent individual participant medians. **B.** Participants responded faster to ambiguous targets when they performed the grasp specified by the nontarget (Compatible trials) than when they performed the opposite grasp (Incompatible trials). These results indicate that parallel motor plans are created automatically in the presence of potential targets. This parallel organization enables faster responses when the plans share an action component (in this case, the direction of wrist rotation). Reprinted from Gallivan et al. (2015). Action plan co-optimization reveals the parallel encoding of competing reach movements. *Nature Communications, 6*(7428), 1-9. Copyright 2015, Macmillan Publishers Limited.

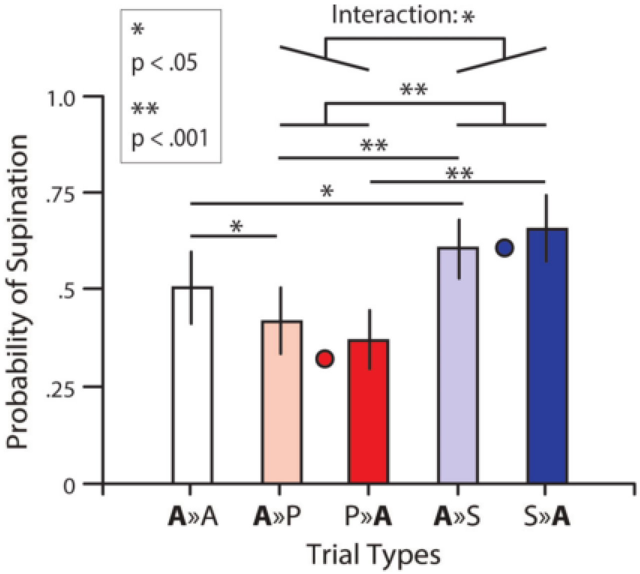

Figure 1.8 – Results from Gallivan et al. (2016). When an ambiguous target was presented with an ambiguous nontarget, participants were equally likely to supinate as pronate (A>>A). When the ambiguous target was accompanied by a non-ambiguous nontarget, however, participants were significantly more likely to perform the co-optimized grasp, regardless of whether the target was presented first (**A**>>P, **A**>>S) or second (P>>**A**, S>>**A**). This result suggests that motor plans are dynamic, and are responsive not only to the precise perceptual environment in which they form but also to environmental changes. Reprinted from Gallivan et al. (2016). The sequential encoding of competing action goals involves dynamic restructuring of motor plans in working memory. *Journal of Neurophysiology, 115,* 3113-3122. Copyright 2016, the American Physiological Society.

Cooptimization of plans has also been demonstrated in terms of spatial proximity. Praamstra et al. (2009) presented participants with potential reach targets separated by varying degrees of spatial angle and measured the voltage of a movement-related potential called the lateralized readiness potential over the motor cortex using electroencephalography. They found that this potential was smaller when three targets was presented versus two, when two targets were presented versus one, and when the spatial angle between two targets was large versus small, which they interpret as representing the greater degree of incompatible components of movement during such trials.

Finally, the affordance competition hypothesis has also motivated re-examinations of phenomena which have previously resisted understanding, such as the distinction between ideational and ideomotor apraxia (Rounis & Humphreys, 2015). Ideational apraxia is the inability to perform actions appropriate to objects, while ideomotor apraxia is the inability to perform appropriate gestures (Heilman et al., 1982). These two conditions have traditionally been understood as representing cognitive and motor impairments, respectively. The affordance competition hypothesis, however, recasts these conditions as representing disturbances to action selection and action specification; ideational apraxia occurs when inappropriate movement parameters are specified, while ideomotor apraxia occurs when inappropriate actions are selected. The affordance competition explains why these two forms of apraxia commonly co-occur (Buxbaum, 2001), as selection and specification are in fact supported by the same neural circuits.

1.5 – Competing Models

The affordance competition hypothesis (Cisek, 2007) is a notable development in the field of decision making because it proposes a fundamental role for the motor system in the decision process. Prior to the hypothesis, the general consensus amongst decision making researchers was that the motor system played no such role. This consensus was reflected in the models that researchers built to explain various aspects of decision making. Although not overwhelmingly successful at explaining decision making, several of these models proved reasonably successful and remain in use by researchers, and so it is worth discussing them in comparison to the affordance competition hypothesis.

Of the models that immediately preceded the affordance competition hypothesis, the most persuasive are of a class of models called sequential sampling models (Gold & Shadlen, 2007). Like the affordance competition hypothesis, these models recognize that the world is both constantly in flux and continuously available to the senses. This means that the information needed to make a decision can, and often must, be gathered across multiple moments in time. Sequential sampling models generally posit, first, that every potential decision outcome is represented by an independent evidence "accumulator", and second, that decisions are made as soon as the accumulated evidence surpasses some kind of threshold. Sequential sampling models can be further divided into two main types: race models (Smith & Vickers, 1988) and diffusion models (Ratcliff & Rouder, 1998). These two models differ on the nature of the threshold that must be surpassed in order for a decision to occur. In race models, each accumulator is independent and possesses its own threshold, with decisions occurring as soon as any one accumulator reaches threshold. In diffusion models, accumulators are compared against each other and do not have independent thresholds; the threshold is instead collective, with decisions reached once the *difference* between accumulated evidences surpasses a threshold.

Race and diffusion models have been applied to both behavioural data (Bogacz, 2007; Smith & Ratcliff, 2004) and neural data (Gold & Shadlen, 2007; O'Connell et al., 2012; Platt & Glimcher, 1999; Shadlen & Newsome, 2001) with success. In particular, these models appear well suited to explaining the time it takes to make decisions of various difficulties, as well as the activation of the parietal lobe during decision tasks. However, as noted by Cisek (2007; Cisek & Kalaska, 2010, these models cannot account for the behaviour of the motor and pre-motor cortex during decisions. If decisions are being reached prior to any motor involvement, then motor regions of the brain should only ever represent the reached decision, but recordings in monkeys have shown that this isn't the case (Cisek & Kalaska, 2002; 2005). They also have difficulty explaining some unusual features of movement which suggest that unselected decision outcomes nevertheless exert influence over motor behaviour (Chapman et al., 2010; Song & Nakayama, 2009) and associated neural signals (Praamstra et al., 2009).

Overall, the affordance competition hypothesis is a promising hypothesis which accounts for several aspects of decision making that cannot be easily explained without invoking the involvement of the motor system. To fully explain the tests of the hypothesis that this thesis reports, however, it will be necessary to review a few further phenomena: perseveration, reference frames, and volition.

1.6 – Perseveration

During psychological experiments, stimuli are usually presented in random order; this prevents anticipation, ensuring that whatever behaviour is produced is a specific reaction to the presented stimulus, and counterbalances for processes that affect performance over long timescales, such as fatigue. In the world outside of the laboratory, however, the random appearance of stimuli is quite rare. Natural objects have inherent dynamics; they do not just appear and disappear, as stimuli do in experiments, but instead persist, moving in continuous and predictable ways. The environment at one moment in time will strongly resemble the environment in the previous moment, meaning that actions that were useful in the previous moment are highly likely to continue being useful in the present moment (Gibson, 1979). Thus, perseveration.

Perseveration is a broad category of effects in which a person's current behaviour resembles a previous behaviour. This can be normal or abnormal. Abnormal perseveration has been most widely studied in cases of brain injury or illness, in which patients become unable to change their behaviour easily or at all. Patients with a frontal lobe injury resulting in hemispatial neglect occasionally demonstrate perseveration on cognitive (Weigl, 1927/1941) or motor tasks (Luria, 1965; Na et al., 1999), while early-stage Parkinson's Disease patients demonstrate perseveration during manual (Ebersbach et al., 1994) or computerized random pointing tasks (Stoffers et al. 2001). Neurologically intact people will also begin to display perseveration when fatigued (van der Linden, 2003).

Perseveration in neurologically-abnormal patients may just be an exaggeration of a general and useful tendency, however. Numerous experiments on healthy individuals, measuring a broad range of movement attributes, have demonstrated a tendency for people to perform a current action in a similar manner to their performance on a previous action. One such attribute is hand orientation; several studies have shown that when presented with an object with two plausible grip orientations, people display a tendency to re-use the grip from the previous trial (Dixon et al., 2012; Dixon & Glover, 2004; Kelso et al. 1994; Rosenbaum & Jorgensen, 1992). In a series of experiments in which people were asked to reach out and grasp discs of varying sizes, Dixon and Glover (2009) revealed that people perseverate grip aperture as well; people produced smaller grip apertures to disks of a certain size following smaller discs than they did following larger discs. This effect was displayed to discs that were presented alone, as well as to discs presented alongside a context disc (in order to eliminate movement biases caused by perceptual illusions). Seen in the light of the affordance competition hypothesis, perseveration appears to merely be a temporally extended case of motor plans being prepared and maintained in order to contribute to future plans, as demonstrated by Masson et al. (2011) and Gallivan et al. (2016).

1.7 – Reference Frames

Objects in the environment can be spatially referenced by organisms in two broad manners: egocentrically, relative to the organism, or allocentrically, relative to the environment. Sense organs, such as the retina or the ears, effectors, such as the eye or hand, and the body itself can all act as the center of egocentric reference, while objects within the environment as well as fixed aspects the environment itself, such as the horizon, can act as the center of allocentric reference (Colby, 1998; Colby et al., 1996; Gibson, 1979; Graziano et al., 1994; Graziano & Gross, 1994, 1995, 1998). In order to use senses to guide actions, organisms must make use of all of these references frames.

The manner in which brains implement these reference frames is well-established: neurons have receptive fields, and are primarily active when they receive inputs commensurate with those receptive fields. For example, neurons in the visual cortex selectively fire when stimuli appear in a particular region of visual space. As a result of being tuned to this region of space, these neurons in a sense "know" where a stimulus has appeared relative to the retina. At a larger level, visual areas of the brain can also be distinguished in this manner; information from particular regions of visual space is relayed to non-random locations within the visual cortex, resulting in what are called retinotopic maps (for reviews, see Felleman & Van Essen, 1991;

Tootell et al., 1998; or Wandell & Winawer, 2011). At a fine and a gross level, visual information is spatially referenced to the retina.

When it comes to motor neurons, however, the situation is different. The neurons responsible for executing the movements of effectors must ultimately reference those movements according not to the retina, or to any other sense organ, but to the effector itself. As far as effectors are concerned, the only thing that matters, spatially, is the vector of movement. If I want to reach out and grasp my by-now well-used teacup with my hand, all that matters is the position of the cup relative to my hand; I can change the visual location of the cup by moving my eyes and my head, or I can close my eyes entirely, and it makes no difference to the vector of movement that must be executed in order to successfully grasp the cup. The problem, then, is this: in order to perform visually-guided actions (or actions based on visual memory), brains must somehow transform retina-centered information into effector-centered information.

The part of the brain responsible for these transformations appears to be the dorsal stream, in particular the parietal cortex. Parietal cortex neurons appear to be involved in representing objects in numerous reference frames, including eye, head, and limb-centered space (Colby, 1998; Colby & Goldberg, 1999; Jeannerod et al., 1995). Neurons in the parietal cortex have been found to represent saccade direction (Snyder et al., 2000), and arm reach direction (Andersen et al., 1999; Andersen & Buneo, 2003; Kalaska & Crammond, 1995), with activity increasing when objects are within reach versus out of reach (Gallivan et al., 2009). Damage to the parietal cortex can result in patients demonstrating neglect to stimuli in peripersonal space, within reach, or in extrapersonal space, out of reach (Bisiach et al., 1986; Cowey et al., 1994; Pizzamiglio et al., 1989); peripersonal neglect can sometimes occur when responses to stimuli are required without being present when observation alone is required (Pizzamiglio et al., 1989).

To summarize, visual information in a retina-centric reference frame must be transformed into effector-centric reference frames into order to produce guided action. Visually-guided tasks must contain a transformation element if action is to be performed successfully. The system that performs these transformations is the dorsal stream, in particular the parietal cortex, which represents numerous reference frames.

1.8 – Spatial Attention

The visuomotor transformations that organisms must engage in to produce actions can be very complicated, especially when their environment contains numerous opportunities for action. Therefore, the brain facilitates this process using the mechanism of spatial attention. Spatial attention is a subtype of attention which allows people to attend to a particular region of space. Many studies have shown that attending to a region of space results in faster and more accurate responses if a target appears there (Eriksen & Hoffman, 1972; Posner, 1980; Posner et al., 1978; 80). Spatial attention is both voluntary and involuntary; although people can consciously choose to attend to a particular region of space or to particular objects (James, 1890), spatial cueing experiments have shown that stimuli appearing in the periphery of the visual field are capable of automatically capturing attention and orienting people towards them (Posner, 1980; Posner & Cohen, 1984; Remington, 1980).

Different types of actions seem to utilize different forms of attention, however, with visually-guided actions making greater use of automatic attention but memory-guided actions making greater use of voluntary attention (Armstrong & Singhal, 2010; Goodale, 2008; Kok, 2001; Liu et al., 2003; Yucel et al., 2005). In Armstrong and Singhal (2010), for example, participants performed a dual task paradigm (Pashler, 1994) featuring an auditory oddball task and a modified Fitts (1954) aiming task in which aiming was either visually-guided or memory-guided, all while undergoing electroencephalography (EEG). EEG uses electrodes positioned over the scalp to detect the underlying cortical activity with millisecond precision. Averaged over many identical trials, EEG waveforms combine to form event-related potentials (ERPs), which are time-dependent deflections in amplitude reliably associated with particular brain regions and neural processes. Armstrong and Singhal (2010) compared two ERPs between the aiming conditions, the P300 as well as the auditory mismatch negativity (MMN). The P300 is a positive deflection in the waveform which occurs 300ms or more after the presentation of a visual target and is generally thought to reflect voluntary attention processes (Johnson, 1993; Kok, 2001), while the auditory MMN is the difference in the waveform between target tones and non-target tones in the unattended ear (in the oddball paradigm, participants are presented with target and non-target tones through both ears but are instructed to respond to targets in one ear only) and is generally thought to reflect automatic attention processes (Näätänen, 1990; 1992; Yucel et al., 2005). The results of the experiment showed that visual and memory-guided actions differentially affect these two ERPs, with visually-guided actions affecting the automatic MMN and memory-guided actions affecting the voluntary P300. Thus, visually-guided actions are especially likely to be affected by variations and biases in automatic attention which might enhance or reduce the amount of attention a target elicits.

A series of relevant experiments by Handy et al. (2003) demonstrates that automatic attention is not uniformly effective across the visual field, but is instead spatially biased. In these experiments, right-handed participants were presented with two images of objects which were either graspable (such as a screwdriver) or non-graspable (such as a goat) and were asked to respond to a target which subsequently appeared atop one of the images. Participants performed two experiments while undergoing EEG. In this case, Handy et al. were looking for an ERP called the P1, so-called because it is a positive deflection which typically occurs over the occipital cortex about 100ms after a visual stimulus is presented. The P1 is known to be larger in amplitude when a stimulus appears in an attended location versus an unattended location (Van Voorhis & Hillyard, 1977), making it possible to infer the relative amount of attention being paid to various stimuli or locations depending upon P1 amplitude (Handy & Mangun, 2000). In the first experiment, the P1 was found to be larger in amplitude for targets presented atop images of graspable objects, but only when the graspable object was presented within the right visual field. In the reverse presentation, with the graspable object presented in the left visual field and the non-graspable object presented in the right, no amplitude differences were apparent. A second experiment replicated and extended this finding, discovering that the same asymmetry occurs along the vertical axis with graspable objects eliciting a larger P1 within the lower hemifield but not within the upper hemifield, while third experiment using functional magnetic resonance imaging (fMRI) found that graspable objects within the right visual field selectively activate two regions closely associated with manual actions, the dorsal premotor cortex (PMd), and spatial attention, the intraparietal lobule (IPL). A follow-up experiment using only left-handed participants did not replicate the left-right P1 asymmetry, but did find a behavioural asymmetry, with graspable objects prompting faster response times in the left visual field but slower response times in the right visual field (Handy & Tipper, 2007).

Additional complications are introduced when participants perform saccades during a task. Extensive research has shown that spatial attention is used in planning and executing saccades (Hoffman & Subramaniam, 1995), and that while spatial attention and gaze direction can be dissociated during fixation, making a saccade to a particular location necessarily redirects spatial attention to that location (Hoffman & Subramaniam, 1995; Rayner, 2009) even when those saccades are very small (Engbert & Kliegl, 2003; Hafed & Clark, 2002). Attention is necessary when making saccades because visual scenes often contain many potential saccade targets (Kowler, 2011) and making an accurate saccade takes effort commensurate with the fidelity of the visual environment (Steinman et al., 2003). Making a saccade to a spatial location notably increases performance to targets at that location (Hoffman & Subramaniam, 1995), even when the saccades are self-directed rather than cued (Wilder et al., 2009). This property of saccades is likely tied to the motor system for the hands in some way; during reaches, saccades arrive at the target location prior to the arm, suggesting that such saccades are meant to facilitate guidance of the arm (Johansson et al., 2001). Similar saccade patterns occur even when people observe the reaches of other people (Flanagan & Johansson, 2003; Rotman et al., 2006), which may indicate that saccades are automatically linked to motor plans, regardless of whether those plans are self-generated or emulated (Rizzolatti et al., 2001). Neurons

Collectively, these results indicate that the visuospatial location of a stimulus matters when it comes to orienting one's attention and preparing a manual response, and that identical stimuli can nevertheless have different neural and behavioural consequences depending upon their visual and spatial locations, the modes of interaction.

1.9 – Volition

Most psychological experiments provide instructions to participants about how, when, and if to act. Participants are presented with stimuli, and are then required to react to that stimulus in a specific way. In these kinds of experiments, any reaction which deviates from the expected reaction is considered an “error” and is discounted. Although such instruction is often necessary given the inferences that the experimenters are attempting to achieve, these kinds of stimulus-driven actions represent only a small proportion of the actions that people normally perform outside of the laboratory. The change of a traffic light from red to green, for example, tells a waiting driver that she must press the accelerator with her foot. In most real-world circumstances, however, people must decide for themselves how to act. A green light may tell a driver to accelerate, but it doesn’t tell her whether to drive straight or to turn. There are no instructions telling me which hand I should use to grasp a teacup on my desk, or when I should take a break from thesis-writing to make more tea; I must decide these things for myself, internally. These actions are voluntary actions. Whether such actions are ultimately voluntary is a subject of much philosophical discussion (for a few of the many, many opinions on the concept of free will, see Dennett, 1984; 1991; Descartes, 1641/1996; Hume, 1748/2008; Kant, 1788/2004; Leibniz, 1710/1951; Libet, 1999; Mele, 2006, 2009; Nagel, 1989; Schopenhauer, 1839/1999; or Wegner, 2002); nevertheless, all that is important for the purposes of this thesis is that stimulus-driven actions can be distinguished from internally-driven actions. Besides the intuitive comprehensibility of this distinction, internally-driven actions have unique consequences for perception, as exemplified by the phenomenon of chronostasis in which clock hands temporarily appear to stop moving following saccades (Park et al., 2003; Yarrow et al., 2001).

Experiments contrasting voluntary and cued or stimulus-driven actions have demonstrated that voluntary and stimulus-driven actions are supported by anatomically-distinct neural circuits. The premotor cortex is functionally divided into lateral and medial portions, with the lateral premotor cortex involved in producing stimulus-driven actions and the medial premotor cortex involved in producing internally-driven actions (Cunnington et al., 2006; Filevitch et al., 2013; Goldberg, 1985; Lau et al., 2004, 2006; Thaler et al., 1995). Two recent experiments by Becchio et al. (2014) reveal that, behaviourally, voluntary and stimulus-driven movements also display distinct kinematic signatures. In the first experiment, participants performed reaching movements to either a small or large target under a voluntary condition, where participants were free to determine whether, when, and what target to reach for, and a cued condition in which these components of movement decision-making were decided for them. Participant movements were monitored with an infrared tracking system, with the results showing differences in numerous features of movement between conditions. In particular, voluntary movements were performed faster than cued movements and maximum grip aperture occurred earlier. In a follow-up experiment, the voluntary condition was decomposed into three conditions in which the whether, when, and what components of decision-making were selectively constrained, with participants still free to determine the other two components. The fully voluntary condition was also repeated as a control condition. The results found that, while fully voluntary movements were faster than fully constrained movements in the first experiment, selective constraint of the what and whether components of decision-making produced movements that were even faster than fully voluntary movements (Figure 1.8). Furthermore, selective constraint of the what and when components resulted in an earlier maximum grip aperture than fully voluntary movements (Figure 1.8). These results suggest that the various components of movement decision-making do not uniformly influence the various features of the resulting movement, but instead selectively exert influence on certain features. For instance, the overall duration of a movement appears to be influenced by the nature of a decision about what object to reach for, but not by decisions about when to reach. This makes intuitive sense, as it is hard to imagine why reaching for an object at one moment versus another would have any effect on movement duration if all other aspects of the decision remain the same.

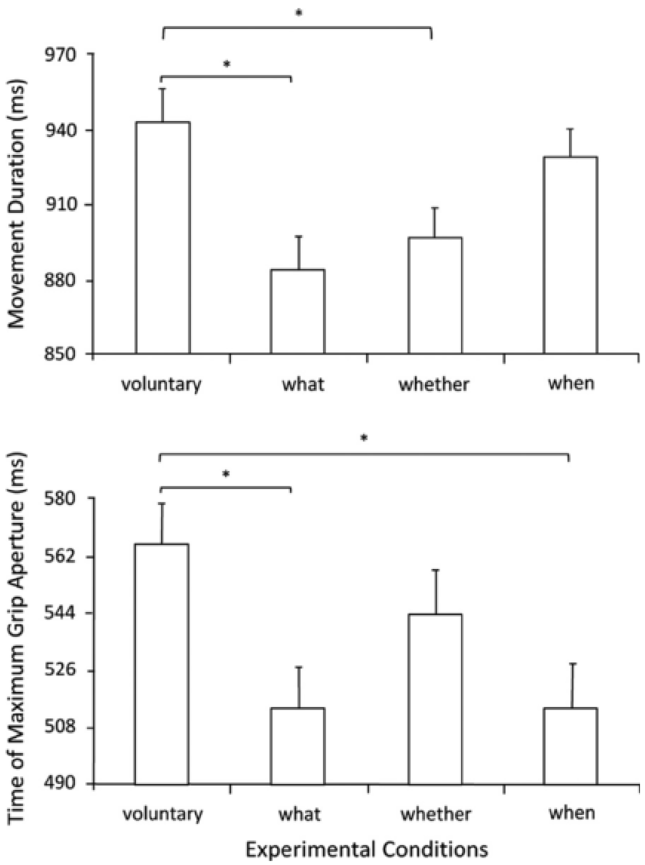

Figure 1.9 – Results of the second experiment by Becchio et al. (2014). Participants were presented with a large object and a small object on each trial. Each trial consisted of three decision components: whether to reach and grasp an object, when to reach, and what object to reach for. In three conditions, each of these components was selectively constrained, leaving the other two components to be decided by the participant. In a fourth condition, all three components were decided by the participant. The results showed that relative to fully voluntary actions, constraining a component resulted in faster movements, a faster time to maximum grip aperture, or both. The "voluntariness" of a decision doesn't just affect internal processes leading to motor action, it also affects performance of the action itself. Republished from Becchio et al. (2014). The kinematic signature of voluntary actions. *Neuropsychologia, 64*, 169-175. Copyright 2014, Elsevier Ltd.

Kinematic differences between voluntary and cued actions presumably occur due to differences in their underlying circuitry, however the exact relation between the circuitry and the behaviour is currently unknown.

1.10 – Summary

We are now prepared to consider all aspects of the three experiments reported in this thesis. These experiments are an attempt to behaviourally test the affordance competition hypothesis of Paul Cisek (2006, 2007; Cisek & Kalaska, 2010), which claims that multiple potential movements are prepared simultaneously whenever there exists multiple opportunities for action. This action preparation takes place within the dorsal stream, which is specialized for the transformation of information from sensory reference frames into movement reference frames; these transformations are necessary for accurate movement. Finally, movements to targets can be either cued or voluntary, with each type of movement utilizing distinct neural circuitry and producing distinct behaviour.

The three experiments reported in this thesis proceeded as follows. In Experiment 1, participants were asked to reach out and touch a circular target in one of eight lateralized positions on a computer touch screen, using their choice of effector (the left hand or the right hand). Participants were expected to produce an approximately equal proportion of left and right hand responses to targets closest to the middle of the screen while favouring the ipsilateral hand for more lateralized targets. As a result, these central targets were also expected to produce the longest response times due to greater competition between the movement plans for each hand. Participants were also expected to exhibit a “switch cost” whenever their response hand was different from the previous trial. In Experiment 2, participants performed a similar task, except targets were preceded by a fixation point on either the left or the right side of the screen. This arrangement varied the direction of the saccade that participants were required to make to some targets while keeping the direction of the hand reach consistent.

Participants were expected to produce faster response times when the saccade direction and the reach direction was the same rather than opposite. Finally, in Experiment 3, fixation points were preceded by a colour cue, which was either instructive of the hand participants were required to make, or irrelevant. This experiment provides a direct contrast of movements to targets during voluntary and cued actions. Following from Becchio et al. (2014), voluntary response times were expected to be faster overall than cued response times. In all three experiments, it was expected that the proximity of the target location to the hands would influence participant behaviour, with targets close to the center of the screen producing roughly equal numbers of voluntary left and right hand actions with slow response times due to the need to select between motor programs for both hands, while more lateralized targets towards the edge of the screen were expected to produce mainly fast actions of the ipsilateral hand.

2 – Methods and Results

Three experiments are reported in this thesis. In all three experiments, participants performed the procedure while wearing a high-density 256-channel Geodesic Sensor Net (Electrical Geodesics Inc., Eugene, OR), which was connected via wires to an amplifier. These sensor nets produce electroencephalograms (EEG), which represent the electrical activity of the brain, particularly that of the cortex. When EEGs are measured during repeated performances of a task, the average of the measured activity produces phenomena known as event-related potentials (ERPs). ERPs are positive or negative changes in electrical voltage which are time-locked to a neural event, such as stimulus onset or response onset. Differences in the amplitude or the latency of ERPs are regularly used by neuroscientists to make inferences about how the brain performs different mental acts. Participants in all three experiments wore EEG nets for this purpose; however, none of the results are reported in this thesis. Data reported in the thesis is confined to psychophysical, behavioural measures of performance such as decision outcomes, reaction time, movement time, and response accuracy, and no further mention of EEG or ERPs will be made from hereon.

Figures and tables presented in this section display the mean and the standard error of the mean (SEM) for each condition, except where noted.

2.1 – Experiment 1

2.1.1 – Participants

Twenty-one (21) people participated in this experiment, which took place at the University of Alberta. Two participants were removed from analysis due to touchscreen calibration errors, leaving 19 participants to be analyzed. Some participants were undergraduates and received course credit for their participation, while others were graduate students who received $10 CAN per hour. Participants were asked to identify their ages, which ranged from 16-58 (mean = 25), as well as their sex (13 male, 8 female). Participants also completed the 10-item Edinburgh Handedness Survey (Oldfield, 1971). Participant L.Q. scores ranged from +20 to +100 with a mean of +81, meaning that all participants identified themselves as right-handed, most of them strongly. All participants had normal or corrected-to-normal vision. Written informed consent was obtained prior to the start of the experiment in accordance with the University of Alberta's ethics review board and the Declaration of Helsinki. Participants were told the procedure but not the purpose of the experiment.

2.1.2 – Procedure

Participants were seated at a table in an electrically-shielded and sound-attenuated room and centered in front of a 4-button keypad (Psychology Software Tools, Sharpsburg, PA) as well as a 430.4mm x 270.3 mm computer-linked touchscreen. At the start of the experiment, participants positioned themselves at a distance from the screen where their fingers could rest comfortably upon the keypad. The distance from the resting position of the fingers to the touchscreen was kept constant at 30cm. A black curtain covered the wall behind the touchscreen and the computer was located underneath the table in order to limit the visual complexity of the environment while participants faced the touchscreen. The experimenter was not present in the room while participants performed trials, and entered only during designated break periods in order to address participant issues with the experiment and to confirm that the participant wished to continue the experiment.

The experiment was written and run in E-Prime presentation software version 2.0 (Psychology Software Tools, Sharpsburg, PA). Participants were required to begin each trial with the index fingers of their left and right fingers pressing down upon the outer two buttons of the keypad. Each trial presented participants with a single black, circular target (radius 11mm) against a white background in one of eight lateralized locations on the touchscreen. Four target locations were located to the left of the screen's vertical midline, while four were located to the right. The centers of each target location were separated by a horizontal distance of 15mm, except for the two central targets which were separated by 30mm. When a target appeared, participants were required to lift either a finger from the keypad, reach out, and touch the target with their finger, all while keeping their other finger firmly pressed. The target stayed onscreen until the touch occurred. Once the target was touched, participants returned their finger to the keypad. The next trial began two seconds after participants pressed the keypad. Participants were free to use either hand on any trial, and no indication was given by the experimenter as to what pattern of responses was desired.

Targets appeared 28 times in each of the eight target locations, for a total of 224 trials. The order of presentation was random for the totality of the experiment. Participants were given a break every 56 trials for a self-determined period of time.

2.1.3 – Data Analysis

Hand use, response time (RT), movement time (MT), and response accuracy (RA) were measured for each trial. RT was defined as the time between target onset and the lifting of a finger from the keypad, MT was defined as the time between the lifting of the finger and contact with the touchscreen, and RA was defined as the straight-line distance between the point of contact and the center of the target; Hand Use refers to whether the left or right hand was used to perform the trial. Trials were excluded from analysis if they met any of the following criteria: an RT or MT less than 50ms or greater than 2000ms, an RT or MT greater than 3 standard deviations from the participant's mean RT or MT, an RA worse than 50 pixels from the center of the target, or if the participant lifted both fingers from the keypad at any time during the trial. When participants only used one hand for all trials of a target, missing data was compensated for by assuming the average of all other participants for that particular hand x target combination.

Hand use data was analyzed in two ways. First, general linear mixed-effects models were fit to the choice of hand for each target position using the binomial family. Models were fit in R (R Core Team, 2017) using the lme4 package (Bates et al., 2018). Whether participants switched their hand choice from the previous trial was then added into the model, giving the likelihood that participants used their right hand for each target position (reported in log odds) as well as the likelihood that they switched or repeated their hand choice for each position. There are a couple of reasons for reporting hand choice in log odds rather than in proportions for this experiment. Unlike proportions, the log odds scale is insensitive to floor and ceiling effects, both of which were likely to occur for hand use in this experiment due to the high degree of target laterality, nor is the log odds scale vulnerable to averaging artefacts such as Simpson's Paradox, in which the pattern of means for individual conditions or participants produces a contradictory grand mean. Furthermore, a normal analysis of proportions is capable of incorrectly suggesting interactions where none exist, especially in repeated measures designs where relevant effects are not fully independent (Dixon, 2008).

Second, differences in RT, MT, and RA on switch versus repeat trials were calculated in order to determine if persisting with the use of a hand carries performance benefits over switching hands. RT, MT, and RA were also calculated for each hand to each target in order to provide a baseline measure of performance and to determine if the location of the target differentially affected performance for each hand. Repeated measures ANOVAs were performed in order to detect differences in RT, MT, and RA depending upon target location and hand use.

2.1.4 – Results

A general linear mixed-effects model of hand choice revealed that participants were more likely to use their left hand for Targets 1-3 and more likely to use their right hand for Targets 4-8 (Table 2.1). Thus, the crossover point from majority-left to majority-right responses occurred not at the screen midline, between Target 4 and Target 5, but instead slightly on the left side of the screen. The model also revealed that participants were more likely to switch hands for the majority of target positions (Table 2.1). The only positions which elicited roughly equivalent numbers of switch and repeat trials were Targets 3 and 4, the two targets for which the overall hand use likelihood was closest to being equivalent.

Right Hand Use		
Target	Previous Left	Previous Right
1	-1.257 (0.284)	-1.568 (0.252)
2	-0.783 (0.272)	-1.234 (0.245)
3	-0.790 (0.272)	-0.589 (0.238)
4	0.612 (0.255)	0.609 (0.240)
5	2.010 (0.279)	1.302 (0.252)
6	3.092 (0.351)	2.176 (0.276)
7	3.157 (0.352)	2.239 (0.279)
8	3.105 (0.358)	2.465 (0.287)

Table 2.1 – Likelihood of choosing the right hand when the previous choice was left or right for each target, reported in log odds and SEM. A larger value in the Previous Left column indicates a tendency to switch hands, while a larger value in the Previous Right column indicates a tendency to repeat the same hand. Values lesser than zero indicate an overall tendency to choose the left hand for that target, while values greater than zero indicate an overall tendency to choose the right hand.

Analysis of participant RT, MT, and RA revealed three significant results. The first is a main effect of target position on participant RT, *F*(7, 126) = 4.241, $p < 0.001$, as well as an interaction between hand and target position, *F*(7, 126) = 4.323, $p < 0.001$. For post-hoc analysis, positions were collapsed into two categories: centralized targets (Positions 3-6) and lateralized targets (Positions 1, 2, 7, and 8). A paired t-test revealed a significant difference in RT between centralized and lateralized targets *t*(18) = 3.384, $p = 0.003$, meaning that participant RT was faster for lateralized targets than it was for centralized targets.

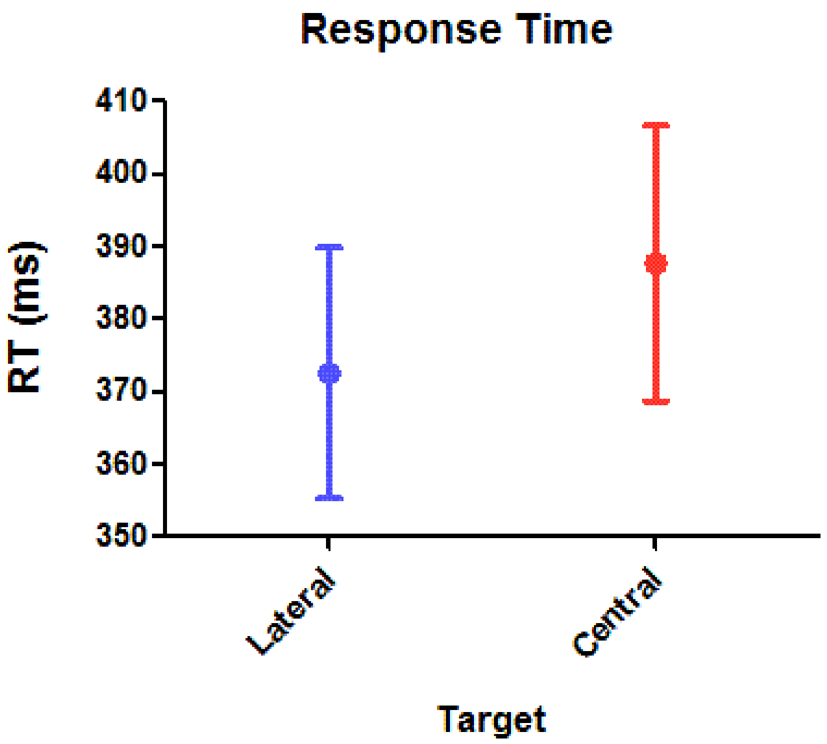

Figure 2.1 – Response times for central targets (the four target locations closest to the middle of the screen) versus lateral targets (the two target locations furthest to the left, and the right, of the screen). RT was significantly longer for central targets (p = 0.003), as per expectations.

The second result is an interaction between hand use and target position when it comes to participant MT, *F*(7, 126) = 2.557, p = 0.017. As the target position was shifted right-ward, left-hand MT became progressively longer, while right-hand MT became progressively quicker.

Finally, an analysis of RA revealed a significant effect of switching versus repeating the use of a hand, *F*(1, 18) = 9.375, p = 0.007. The switch cost was unaffected by target position. Responses were less accurate overall when participants switched hands from the previous trial versus when they used the same hand. No switch costs were observed for RT or MT.

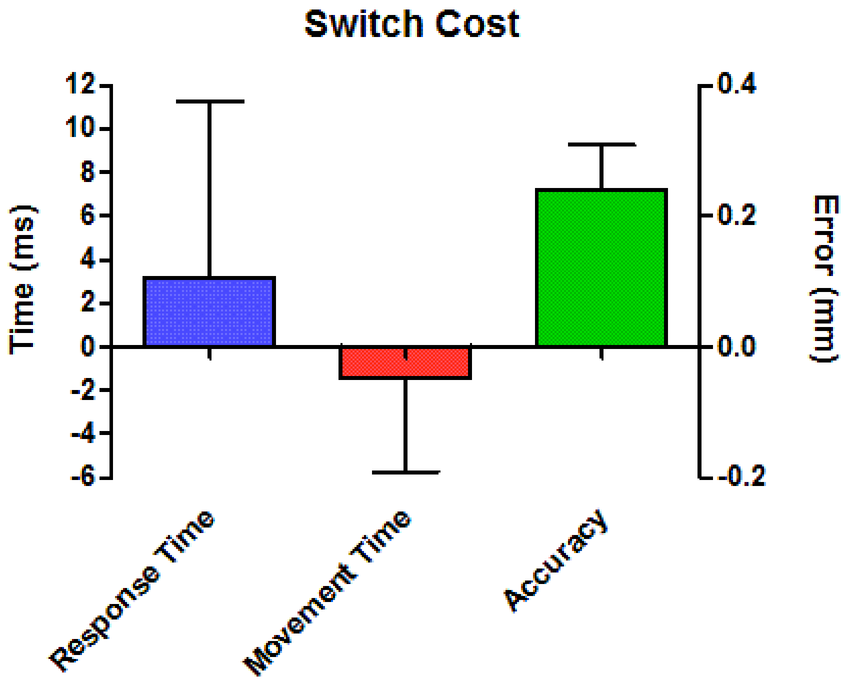

Figure 2.2 – The cost of switching hands from one trial to the next. RA was significantly worse when participants switched hands rather than repeating the use of a hand (p = 0.007). Switching hands did not measurably impact RT or MT.

2.1.5 – Discussion

In Experiment 1, it was expected that central targets (targets 3-6) would produce an approximately equal proportion of left and right hand responses, and that these responses would therefore be slower than responses to lateral targets due to greater competition between the two movement plans. The results generally affirm these predictions. Targets 3 and 4 produced roughly equal numbers of left and right hand responses, and RT was significantly slower for central vs. lateral targets. These results suggest, per the affordance competition hypothesis, that parallel movement plans are created for each potential response during a task and that a response decision is arrived at through a process of competition between them. A switch cost when participants switched hands from the previous trial was also expected, and this occurred in the form of an accuracy cost: participants responded less accurately on switch trials vs. repeat trials.

The hand use pattern that participants produced indicates that their decisions were mainly based on spatial considerations, with right-sided targets producing more right hand responses and left-sided targets generally producing more left hand responses. The fact that participants preferred to switch hands to most targets is probably a consequence of the lateralized target positions and the pseudo-randomized presentation: the more lateralized a target was in a certain direction on one trial, the more likely it was that the previous target was lateralized in the opposite direction. For example, when Target 2 was presented, the odds of the previous trial being presented further to the left were approximately 1/8, while the odds of the previous trial being presented further to the right were approximately 3/4. Thus, the pseudo-random jumping of the target from one side of the screen to the other may have encouraged more hand switching than might be expected during other pointing or reaching paradigms or during natural behaviour. However, it is interesting that the two target positions for which this switch preferences was not expressed happened to be Targets 3 and 4, where left and right hand responses were more or less equivalent. These target positions also fall into the central target category for which RT was slowest. The absence of a strong preference for switching or repeating hands to these targets may further indicate the degree to which central targets afford left and right hand responses in equal measure, necessitating a robust process of competition before a response can be selected.

However, hand movements were not the only movements performed by participants during Experiment 1; they also performed saccades to the target. Since Experiment 1 did not present a fixation cross prior to the target, it was not possible to account for any possible effect of the saccade on hand choice or performance. This is problematic because when a saccade is performed, spatial attention is necessarily redirected towards the location of the new gaze point, with a resulting facilitation of performance at that spatial location (Hoffman & Subramaniam, 1995). If participants performed a saccade just prior to the presentation of a target, then their performance on that trial would have been substantially determined by whether or not the saccade happened to be towards or away from the target location. Experiment 2 was therefore conducted in order to control for the possibility of such saccadic effects.

2.2 - Experiment 2

2.2.1 – Participants

Nineteen (19) people participated in this experiment, which took place at the University of Alberta. All participants were undergraduates and received course credit for their participation. Participants were asked to identify their ages, which ranged from 18-26 (mean = 22), as well as their sex (8 male, 11 female). Participants also completed the 10-item Edinburgh Handedness Survey (Oldfield, 1971). Participant L.Q. scores ranged from +69 to +100 with a mean of +91, meaning that all participants identified themselves as strongly right-handed. All participants had normal or corrected-to-normal vision. Written informed consent was obtained prior to the start of the experiment in accordance with the University of Alberta's ethics review board and the Declaration of Helsinki. Participants were told the procedure but not the purpose of the experiment. No participants from Experiment 1 participated in this experiment.

2.2.2 – Procedure

The procedure for Experiment 2 was the same as for Experiment 1, with a number of exceptions. In Experiment 2, target presentation was preceded by the presentation of a fixation cross in one of two locations, either 30mm to the left or the right of the center of the screen. The number of target locations was reduced from eight to four, 45mm and 15mm to the left and the right of the center of the screen. The fixation cross was presented for 1000ms, followed by a blank screen for 500ms.

Each of the eight possible fixation cross x target combinations was presented 56 times, for a total of 448 trials. The order of presentation was random for the totality of the experiment. Participants were given a break every 56 trials for a self-determined period of time.

2.2.3 – Data Analysis

RT, MT, and RA were measured as per Experiment 1, with one additional factor required due to the introduction of the fixation cross. Although the two outer targets required either right or left saccades regardless of the location of the preceding fixation cross, the two central targets could be preceded by a fixation cross to their left, requiring a saccade to the right, or to their right, requiring a saccade to the left. Thus, on some trials it was necessary for participants to perform a leftward saccade to a target but a rightward hand movement. This condition will henceforth be referred to as Congruency: trials where the target required saccades and hand movements in the same direction are congruent, while trials where the target required saccades and hand movements in opposite directions are incongruent. Repeated measures ANOVAs were performed in order to detect differences in RT, MT, and RA depending upon target location, hand use, and congruency.

Hand Use was measured in terms of proportions rather than in log odds as was the case for Experiment 1.

2.2.4 – Results

Proportions were calculated for each target from each participant's hand use data. All four targets produced right hand proportions greater than 0.5 (Table 2.2). Thus, participants produced majority right-hand responses to all targets, with the proportion of right-hand responses increasing as the target was presented further to the right.

Target	Right Hand Use
1	0.510 (0.079)
2	0.623 (0.064)
3	0.730 (0.052)
4	0.818 (0.056)

Table 2.2 – Proportion of right hand responses and SEM for each target position. Values above 0.5 indicate a majority of right hand responses. Overall, each position produced more right hand responses than left, with right hand use increasing for each rightward position.

An analysis of RT depending upon target position revealed an interaction between hand use and target position, $F(3, 57) = 3.039$, $p = 0.036$. Multiple comparisons did not reveal any significant comparison, however. A paired t-test comparing all right hand responses versus all left hand responses revealed a significant effect, $t(18) = 2.479$, $p = 0.023$. Data for left hand responses to Target 4 were missing from respondents with the longest overall response times but present for respondents with the shortest response times, which likely biased the ANOVA. A collation of target positions resulted in a complete data set as all participants performed some number of left handed responses, thus eliminating this bias. When the two middle target positions were considered separately, analysis revealed a main effect of congruency, *F*(1, 16) = 6.154, p = 0.025. This indicates that participants were quicker to initiate responses to targets when saccade direction and hand movement direction were congruent.

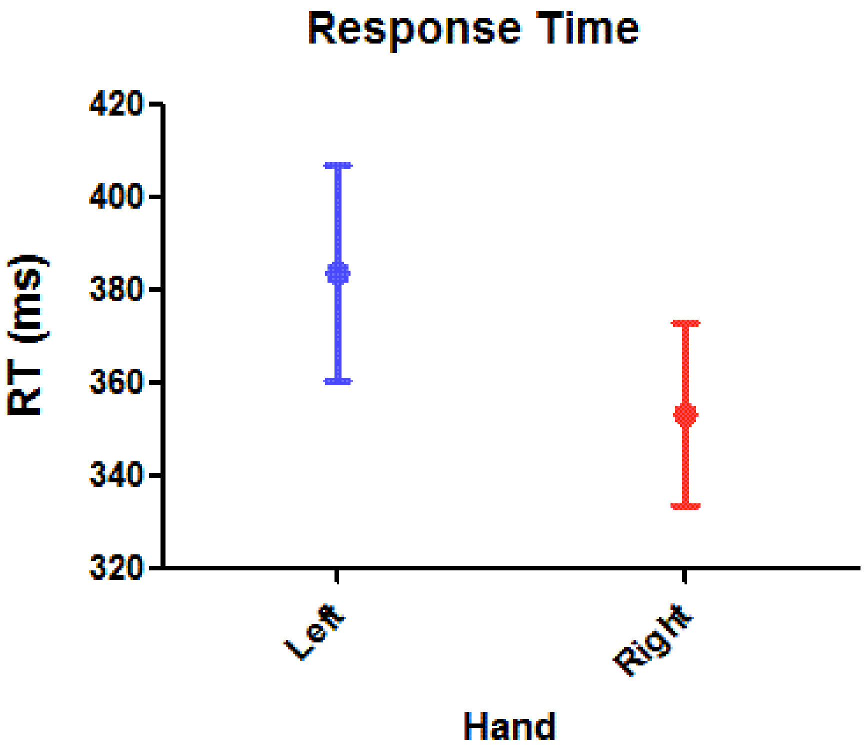

Figure 2.3 – Response times for right hand versus left hand responses across all target positions. Participants performed significantly faster with their right hand than their left (p = 0.026).

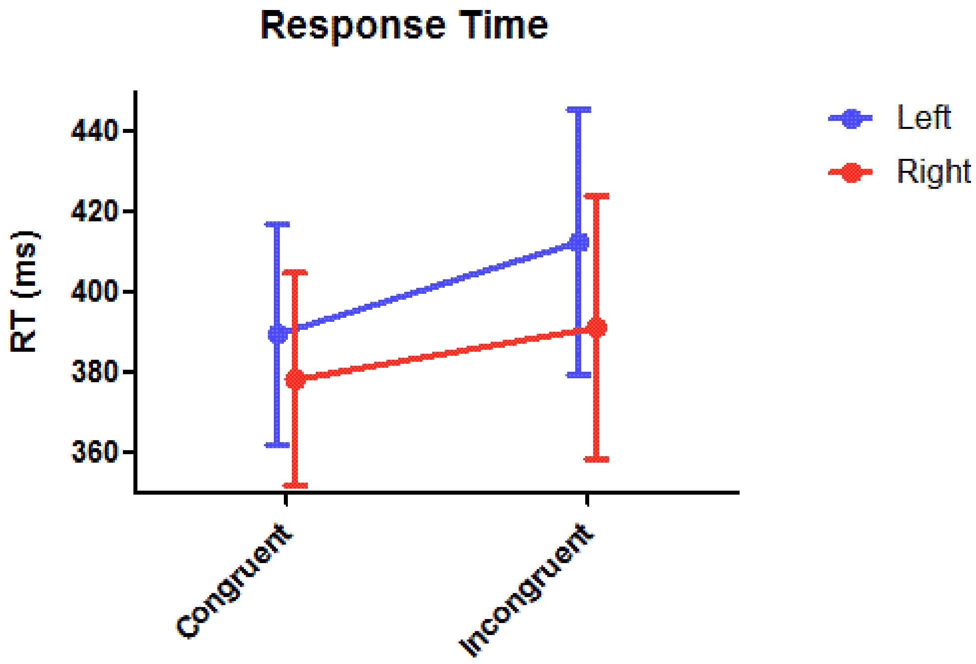

Figure 2.4 – Response times for congruent and incongruent targets, depending upon the hand that was used. Participants performed significantly faster during congruent trials (p = 0.025).

Analysis of RA revealed a main effect of hand use *F*(1, 15) = 5.606, p = 0.032, indicating that participants responded with greater accuracy with their right hand versus their left. No effects involving target position or congruency were observed.

No significant results of any kind were observed for MT.

2.2.5 – Discussion

In Experiment 2, each target was preceded by a fixation cross in one of two lateralized locations in order to account for the influence of saccade direction on hand choice and performance. The results showed that participants responded faster to targets when the saccade and the reach were performed in the same direction. Thus, it appears that the spatial location of a target relative to fixation influences decisions about how to interact manually with it. There are two possible explanations for that influence. According to one explanation, movement preparation for the eyes is interfering with movement preparations for the hands just as movement preparation for one hand interferes with preparation for the other. This interference explanation implies that response competition is effector-independent to some degree: the identity of the effectors preparing movements is less important than the direction in which those movements are being prepared. An alternative, non-competitive explanation makes use of the fact that the location of a target can be described using many different reference frames: target locations in can be described relative to the position of the hand, the head, the point of fixation, the center of attention, another object, etc. In the case of Experiment 2, the relevant reference frames are those relative to the hand and the point of fixation. During congruent trials, the target was on the same side of space relative to the retina as it was to the hand; during incongruent trials, it was not. This reference frame incongruity may have made it slightly more difficult for participants to prepare an accurate movement, resulting in a longer RT. The results of Experiment 2 cannot distinguish between these two explanations, resulting in the design of Experiment 3. In Experiment 3, a new condition was created in which participants were asked to perform a right or left hand movement to each target depending upon the identity of a preceding colour cue. If the reference frame explanation is correct, then a congruency effect should occur during both cued and chosen actions, since the location of the target in fixation-space and hand-space will be the same regardless of the kind of action being performed. If the congruency effect disappears during the cue condition, however, then the competition explanation is more likely to be correct.

2.3 – Experiment 3

2.3.1 – Participants

Eighteen (18) people participated in this experiment, which took place at the University of Alberta. All participants were undergraduates and received course credit for their participation. Participants were asked to identify their ages, which ranged from 18-26 (mean = 20), as well as their sex (8 male, 10 female). Participants also completed the 10-item Edinburgh Handedness Survey (Oldfield, 1971). Participant L.Q. scores ranged from +71 to +100 with a mean of +94, meaning that all participants identified themselves as strongly right-handed. All participants had normal or corrected-to-normal vision. Written informed consent was obtained prior to the start of the experiment in accordance with the University of Alberta's ethics review board and the Declaration of Helsinki. Participants were told the procedure but not the purpose of the experiment. No participants from Experiment 1 or Experiment 2 participated in this experiment.

2.3.2 – Procedure

The procedure for Experiment 3 was similar to that for Experiment 2, again with a few exceptions. Each trial began with the presentation of a colour cue prior to the presentation of the fixation cross. Colour cues were presented in the center of the screen for 250ms, followed by a blank screen for 750ms prior to the fixation cross. Cues were either red or blue. Trials were divided into three blocks (four blocks for five participants). In the first two blocks, participants were instructed to respond with either their left hand or their right hand depending upon the preceding cue colour. Cue signifiers were reversed between the first and second blocks and counterbalanced across subjects, producing equal numbers of left and right-hand responses for all targets. In the third block (as well as the fourth block for five participants), the cues still appeared, but participants were instructed to ignore them and respond with whichever hand they wanted, as in Experiments 1 and 2. These will be referred to as the cue condition and the choice condition. Each block of trials contained 144 trials, for a total of 432 trials (576 for the five participants).

2.3.3 – Data Analysis

Hand use, RT, MT, and RA were analyzed as per Experiment 2, with one additional factor required due to the introduction of the cue. Some trials required participants to respond to the target using a specific hand, while other trials did not. Response proportions were calculated for hand use during the choice condition only. Repeated measures ANOVAs were performed in order to detect differences in RT, MT, and RA depending upon target location, hand use, congruency, and cue.

2.3.4 – Results

The proportion of right hand responses was calculated for each target when responses were chosen, with proportions ranging from 0.452 for Target 1 to 0.822 for Target 4 (Table 2.3). Thus, participants produced majority right-hand responses to all targets except the left-most target, with the proportion of right-hand response increasing as the target was presented further to the right.

Target	Right Hand Use
1	0.452 (0.069)
2	0.640 (0.054)
3	0.747 (0.045)
4	0.822 (0.046)

Table 2.3 – Proportion of right hand responses and SEM for each target position. Values above 0.5 indicate a majority of right hand responses. Overall, each position produced more right hand responses than left except for Target 1, with right hand use increasing for each rightward position.

RT analysis revealed an interaction between hand use and position within the cue condition, $F(3, 51) = 3.513$, $p = 0.022$. Participants initiated responses to left-most targets with their left hand faster than with their right hand, and rightmost targets with their right hand faster than with their left hand. An analysis of congruency revealed no significant results; however, an analysis of central versus lateral targets revealed a significantly slower RT to central targets in the choice condition, $F(1, 17) = 5.061$, $p = 0.038$, as per the results of Experiment 1, but a significantly faster RT to central targets in the cue condition, $F(1, 17) = 4.924$, $p = 0.040$.

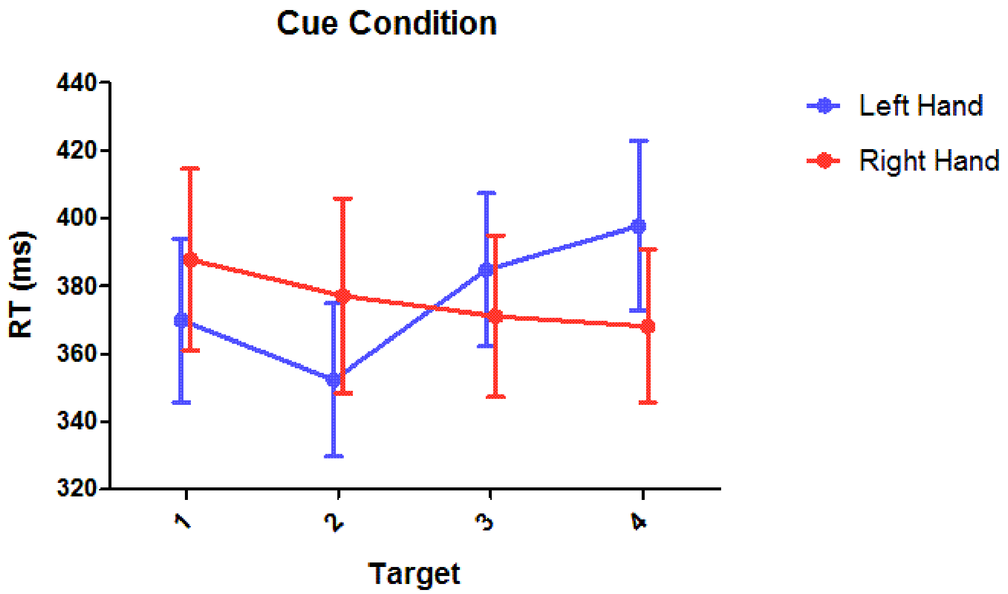

Figure 2.5 – Response times for the right and left hands during the cue condition. The left graph shows individual participant data, while the right graph shows data averages for the purposes of clarity. Statistical analysis revealed an interaction between hand and position, with left hand responses faster for left-sided targets (Targets 1 and 2) and right hand responses faster for right-sided targets (Targets 3 and 4), p = 0.022.

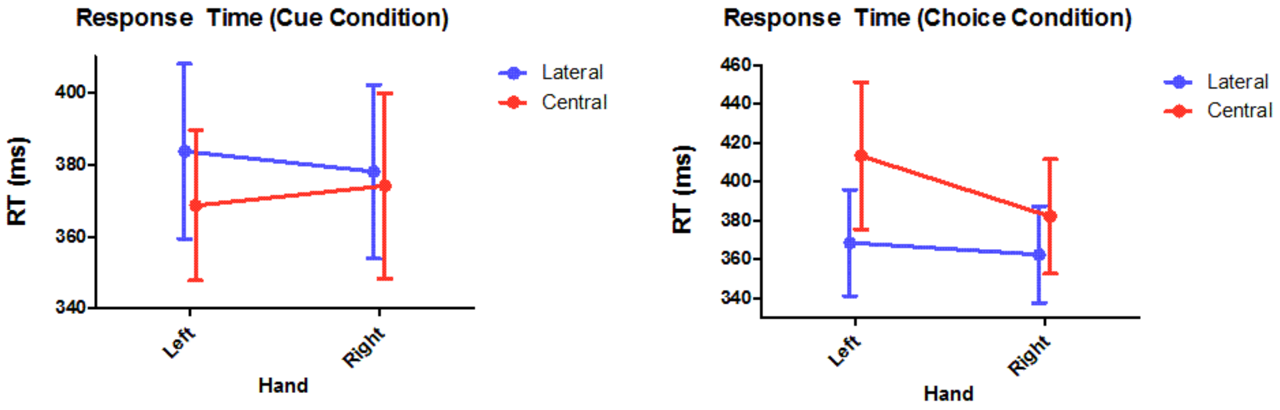

Figure 2.6 – Response times for left and right hand actions to central and lateral targets in the cue and choice conditions. RT was faster to central targets in the cue condition (p = 0.040) but slower to central targets in the choice condition (0.038). Experiment 1 also found slower RTs to central targets during voluntary actions (p = 0.003).

MT analysis revealed an interaction between hand use and position within the cue condition $F(3, 51) = 11.92$, $p < 0.001$. When the target shifted rightwards, left hand movements became progressively slower, while right hand movements became progressively faster. Within the choice condition, there were significant main effects of hand $F(1, 17) = 5.52$, $p = 0.031$ and position $F(3, 51) = 3.12$, $p = 0.034$, as well as a significant interaction $F(3, 51) = 4.007$, $p = 0.012$. Right hand movements were faster than left hand movements, and movements to the left targets were faster than movements to the right targets, except for right hand movements to the right-most target, which was the fastest of all. When just the middle targets were analyzed, MT analysis revealed a main effect of cue condition $F(1, 136) = 5.211$, $p = 0.036$. Participants performed faster movements to the touchscreen when responses were chosen rather than cued.

RA analysis revealed a main effect of hand use within the cue condition $F(1, 17) = 29.16$, $p < 0.001$, indicating that right hand responses were more accurate than left hand responses. Within the choice condition, a main effect of hand was also observed $F(1, 17) = 9.004$, $p = 0.008$. When just the middle target positions were considered, main effects of condition $F(1, 17) = 10.86$, $p = 0.004$ and hand use $F(1, 17) = 17.8$, $p = 0.001$ were observed. Right hand responses were more accurate than left hand responses, and cued responses were more accurate than chosen responses. No congruency effects were observed.

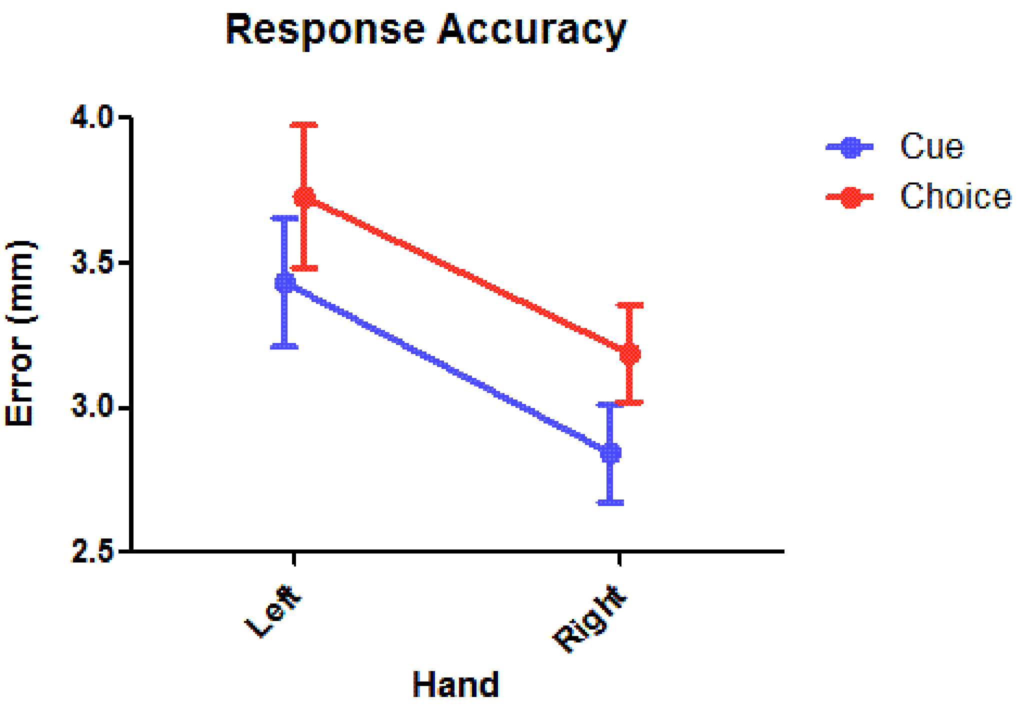

Figure 2.7 – Response Accuracy for central targets depending upon which hand was used and whether hand use was cued or chosen. Error represents the distance between target center and the point where participants contacted the screen. Results showed a main effect of both condition (p = 0.004) and hand (p = 0.001). Participants responded more accurately when hand use was cued rather than chosen, and also responded more accurately with their right hand than their left.

2.3.5 – Discussion

In Experiment 3, the volitional actions from Experiments 1 and 2 were directly compared against stimulus-driven actions via the introduction of a colour cue, which participants could ignore during some trial blocks but not others. This procedure was created in order to test two possible explanations for the congruency effect observed during Experiment 2: a competition explanation and a reference frame explanation. Unfortunately, these explanations still could not be distinguished as the effect did not replicate during the choice condition. Other results, however, showed that voluntary differ from stimulus-driven actions in a number of ways. In particular, participants responded slower to central targets during the choice condition (as they did during Experiment 1) but faster during the cue condition. If the slow RT to central targets during the cue condition is due to increased response competition for these targets, then the effect of competition on performance appears to be large. Responses were also performed more accurately during the cue condition than the choice condition, further suggesting that parallel movement plans interact and interfere with each other.

3 – General Discussion

This thesis reports three experiments, each of which examined several aspects of voluntary motor behaviour in right-handed people. These aspects include response bias, neural competition, reference frame transformations, and perseveration. In Experiment 1, response bias, competition, and perseveration were examined, while in Experiments 2 and 3 reference frame transformations were examined in lieu of perseveration. Experiment 1 presented people with small, circular targets on a touchscreen, which they could respond to with either hand. Experiment 2 introduced a fixation cross in order to control participant's eye movements to the target and vary which visual field targets could appear in. Finally, Experiment 3 introduced a cue condition in which participants were given instructions about which hand to respond with in order to contrast cued and willed performance. Hand Use (for the choice condition for Experiment 3), Response Time (RT), Movement Time (MT), and Response Accuracy (RA) were analyzed for all three experiments. In all three experiments, it was expected that targets near the center or the screen would produce roughly equal numbers of left and right hand responses, while targets near the periphery would produce primarily ipsilateral responses. This difference was expected to result in slower RTs to central versus peripheral targets, due to stronger neural competition between movement plans for the two hands. This prediction was entirely borne out by the results of Experiment 1, but the results of Experiments 2 and 3 were more ambiguous and require deeper consideration.

3.1 – Experiment 1

In Experiment 1, 21 participants responded to a target in one of eight lateralized target positions using their choice of hand. Several predictions were made for this experiment:

1) Participants were expected to produce more ipsilateral responses to targets, with the odds of using the ipsilateral hand increasing with degree of lateralization. This is due to the physical distances that must be traversed when responding ipsilaterally versus contralaterally; ipsilateral hands are simply closer to more eccentric targets than contralateral hands, meaning that movement time is minimized.

2) In accordance with prediction 1, MT was expected to be faster to ipsilateral versus contralateral targets.

3) Participants were expected to produce slower RTs to central targets versus more lateral targets, due to neural competition. Neural competition, as described in detail by Cisek and Kalaska (2002; 2005; 2010; Cisek 2006; 2007), occurs when multiple potential actions are prepared simultaneously, necessitating a resolution process before an action can proceed. Centralized targets ought to be more likely to produce strong competition than lateralized targets due to the participants' lack of a preferred response.

4) Finally, participants were expected to demonstrate perseveration in the form of a performance cost when switching hands from one trial to the next, as well as a repetition effect in which participants tend to repeat their hand choice from one trial to the next. Perseveration, or the tendency to repeat one's behaviour over time, is a common issue in people with impaired cognitive function but has also been demonstrated in cognitively healthy people (Rosenbaum & Jorgensen, 1992; Kelso et al. 1994; Dixon & Glover, 2004; 2009; Jax & Rosenbaum, 2007). This tendency was expected to interfere with the subsequent trial by biasing competition in favour of

the previously-used hand, resulting in faster and more likely use of the same hand relative to the previously un-used hand.

The results in Experiment 1 were largely as expected, with one exception in the case of the perseveration predictions. Participants did indeed produce majority-ipsilateral responses to targets, with the exception of Target 4 (the least lateralized target on the left side of the screen), which produced majority right hand responses. This is likely due to the right-handedness and resulting bias of the participants. Every participant in the experiment identified as right-handed and scored positively on the Edinburgh Handedness Inventory. The likelihood of a right hand response increased at every increment from left to right, so the overall pattern was as expected. If the experiment was repeated with left-handed participants, it’s possible that the opposite pattern would occur, with Target 5 producing a majority left-hand response despite being slightly on the right side of the screen. A somewhat similar experiment to Experiment 1 by Gabbard et al. (1997), which asked participants to grasp a solid object on a table at various equidistant locations between -90° and +90°, found that both left- and right-handed participants displayed a bias towards their preferred hand when the object was presented at the midline, although the bias was somewhat smaller for left-handed participants. It’s also possible, however, that left-handed participants would show no bias or even the same right-handed bias in this experiment as right-handed participants. Numerous experiments have previously shown that some left-handed people are biased towards using their right hands on a wide range of tasks, from classic psychology paradigms such as the Annett pegboard task and dot-filling tasks (Bryden et al., 1994; Steenhuis & Bryden, 1999) to visually-guided grasping (Gonzalez & Goodale, 2009; Stone et al., 2013). Overall, the degree to which people use their preferred hand for tasks seems to increase with task complexity (Bryden & Huszczynski, 2011; Gabbard et al., 2003; Mamolo et al., 2006; Steenhuis & Bryden, 1999). The simplicity of the task performed in Experiment 1 would therefore lend itself to the prediction that left-handed participants would show either no bias or a right-hand bias on this task rather than a left-hand bias.

Interestingly, the handedness bias in Experiment 1 was not reflected in performance, with participants displaying no overall differences in RT, MT, or RA depending upon hand use. However, it is possible that participants only produced equal levels of performance by minimizing use of their left hand, and that forced use of the left hand for contralateral targets would reveal a disparity. This possibility is explored in Experiment 3.

Per the second prediction, participants produced longer MTs for contralateral versus ipsilateral targets. MTs were longer for left hand movements to right side targets, and vice versa. This reflects the varying physical distances that each hand had to move in order to reach the targets. This MT result explains why participants largely chose to respond to targets with the ipsilateral hand: it's just faster.

The third prediction was also borne out. Overall, RTs were about 15ms faster to lateralized targets than they were to central targets (Figure 2.1). This difference supports the hypothesis that participants were simultaneously planning left and right hand actions during the task. When multiple potential responses are planned but only one response is possible, a process of competition is necessary to resolve this problem, and this process takes time commensurate with the relative strengths of those plans. The relative strengths of the potential movement plans are expressed in the participants' behavioural choices, where the odds of choosing a particular hand were much closer to even for centralized targets than they were for lateralized targets.

Although several experiments in humans have previously demonstrated some form of response competition, none of these experiments have allowed for any sort of willed behaviour on the part of their participants. An experiment by Praamstra and colleagues (2009), for example, presented participants with one, two or three arrows per trial prior to target presentation. Each arrow pointed to a unique potential target location, and there were six potential target locations in a ring formation, three to the left of the participant's body and three to the right. The result of this experiment was that reaction time increased with the number of potential target locations, which the authors interpret as evidence of multiple response planning. However, every arrow presented during a trial pointed in the same direction, and participants were required to respond with their ipsilateral hand, meaning that on no trials were participants ever required to plan movements with both hands simultaneously. Although participants experienced a period of uncertainty between arrow and target presentation, ultimately no decisions were ever made by the participants in this experiment. A follow-up experiment, in which two arrows pointed towards targets with either a shallow or wide angle between them, demonstrated longer reaction times for the wide angle targets than the shallow angle targets, which suggests that the variable that competition acts upon is the vector of movement required by each movement plan.

Another experiment by Chapman et al. (2010) presented participants with one or two possible target locations and asked participants to reach for them with their right hand before the target was revealed. This experiment resulted in no RT differences between the one and the two-target trials, even though participants presumably planned two movements in the two-trial condition versus only one in the one-target condition. The two-target condition is unusual, however, in that movement onset was required before the true target location was revealed. This aspect of the trial may have encouraged rapid response times despite competition, with movement tracking data revealing that participants took into account both target locations in their initial movement trajectory before adjusting their movement mid-flight. Movement plans prior to movement onset are known to be fairly simple, with movements relying heavily on online sensory feedback to achieve precision (Flanagan & Wing, 1997; Wolpert & Kawato, 1998; Cisek (2005). Online control of movements is especially important when objects in the environment are either moving or out of visual contact, as the targets were here. In Experiment 1, resolving competition was necessary before movement could take place, but in the Chapman experiment, it was the reverse. A recent experiment attempted to model decisions as both cognitive and action-based, finding evidence only for the former (Wispinski, 2017). This experiment utilized a more cognitively complex task than Chapman et al. (2010) and Praamstra et al. (2009), however, requiring participants to monitor two flashing circles of changing luminance at two levels of difficulty and report if one was brighter. Compared to this task, the three experiments reported in this thesis are all cognitively sparse: participants did not have to attentively monitor any aspect of their environment over any period of time and there were no right answers to seek or wrong responses to inhibit. Participants were simply presented with a target, which never changed or disappeared, and were asked to touch it with whichever hand they felt like. The exercise of will is another unique aspect of the experiments in this thesis; in no other experiment on this matter have participants been allowed to freely choose their responses as opposed to following task rules. The hypersimplicity of the experiments in this thesis seems the best and most likely way to detect competition between action representations without invasive methodologies. When all potential values for a cognitive-based decision system to act upon have been denied to a decision-maker or declared irrelevant, what ought to be left for them to decide with is an action-based system.

Only the final prediction of Experiment 1, the expectation of perseveration in the form of a repetition effect and a switch cost in terms of RT, was defied. Repetition effects have been previously observed for a variety of motor parameters, particularly grip selection (Dixon et al., 2012; Dixon & Glover, 2004; Kelso et al. 1994; Rosenbaum & Jorgensen, 1992), and it was thought that participants in this experiment might demonstrate a repetition effect for hand selection, even though the simplicity of the motor actions being performed meant that the benefits of perseveration were likely to be minor. Instead of a repetition effect, however, Experiment 1 instead displayed a switch effect to most target positions (Table 2.1). In retrospect, the increased likelihood of switching hands is not especially surprising considering the lateralized target locations and the pseudo-random presentation sequence. In this paradigm, the more lateralized a target was in a particular direction, the more likely it was that the previous and subsequent trials would be lateralized in the opposite direction. For example, if Target 2 was presented on one trial, the likelihood of the previous target being presented further to the left was approximately 1/8, whereas the likelihood of the previous target being presented further to the right was approximately 3/4. Given the overall pattern of responses, in which right hand responses became more likely with each rightward target location, it is easy to see how left hand responses to the left-sided targets would be primarily followed by right hand responses and vice versa. Not all targets elicited a switch preference, however; for Targets 3 and 4, the likelihood of switching hands was roughly equivalent to the likelihood of repeating the previous hand. This could be due to the pseudo-random nature of the paradigm having a lesser impact on central targets, for which the likelihood of the previous target being presented to the left versus the right is closer to being equivalent. If that were the case, though, then Targets 4 and 5 might be expected to display similar switch likelihoods. The fact that they do not suggests that the lack of a switch effect for Targets 3 and 4 may instead be due to the right and left response likelihoods at those positions, which were close to equivalent. The lack of a switch effect at these locations, alongside the lack of a hand preference, therefore strengthens the argument that central targets afford left and right hand responses more or less equally, necessitating a lengthy process of competition before a response can occur.

When it comes to switch costs, the preservation of movement plans from one trial to the next was expected to facilitate more rapid use of the same hand, but no difference in RT or MT was observed for switch versus repeat trials. However, a switch cost was observed in terms of RA (Figure 2.2). A deeper consideration of the affordance competition hypothesis at a neural level will show why this is less surprising than it initially seemed. The key insight necessary to understanding this result is that the most important information prior to movement is movement direction, which need not be precise.

Neurons in the cortex often exhibit “tuning”, meaning that they preferentially respond to certain perceptual or motor parameters. Neurons in the motor and premotor cortex of monkeys, for example, exhibit tuning for arm movements in a particular direction (Bastian et al., 1998, 2003; Cisek & Kalaska, 2002, 2005; Cisek et al., 2003; Georgopoulos et al., 1982; 1968). The tuning curves of these neurons overlap, such that they collectively represent movement in all directions. When one or more potential reach targets are presented, neurons tuned to each direction display strong activation, resulting in the overall activity of the population representing all available reach options. These reach options, by virtue of requiring movements in different directions, are mutually exclusive; one cannot reach to one's right and one's left simultaneously using a single limb. Thus, an additional process is required to deactivate neurons tuned to all directions but one. To explain how this happens, Paul Cisek (2007) has proposed a model in which tuned neurons excite neurons with similar tuning functions while inhibiting neurons with dissimilar tuning functions. The initial activation level of each neuron key to determining the outcome is provided by a variety of information sources, such as visual information from the occipital lobes specifying the location of the targets and goal information from the frontal lobes assigning value to targets. Whichever reaching movement is ultimately performed is determined through this process.

In Experiment 1, there was only one target presented per trial and no goal; participants did not receive any benefit or loss from using one hand rather than the other, and although participants were all right-handed and showed a right hand bias in their responses, no actual performance advantage was observed for the right hand. However, the direction of the two response options was still in conflict; each target required a slightly different movement from one hand versus the other. This conflict was most marked for the central targets, which required rightward movements of the left hand but leftward movements of the right hand, which probably explains the longer RTs for central targets. The reason why switching hands did not come with an RT cost is because in Experiment 1, movement directions were not necessarily consistent between trials. A participant could perform a right hand response to Target 1 on one trial, requiring a lengthy leftward movement of the hand, then perform another right hand response to Target 8, requiring a length rightward movement of the hand. The hand may have been consistent across two trials, but movement direction was not. Thus, preserving a movement plan from one trial to the next was not actually useful in facilitating rapid movement, since movement direction, the important variable in competition, was often inconsistent between trials.

When a preserved movement plan may have come in handy, however, was during the movement itself. Arm movements require stability and precision control via (primarily) visual and proprioceptive feedback (Barkley et al., 2014; Desmurget & Grafton, 2000; Miall & Wolpert, 1996; Monaco et al. 2010; Rossetti et al., 1995; van Beers et al., 1999; Wolpert et al., 1995; Wolpert & Ghahramani, 2000), and although the targets were extremely simple, they were also small. Thus, a considerable degree of precision was required in order to touch them at or near their center. Prior to the experiment, participants were asked to perform their movements "as quickly and accurately as possible". During everyday actions it is possible for people to increase their accuracy by decreasing their movement speed, resulting in more time to make fine adjustments to the movement trajectory, but in Experiment 1 this possibility was closed to the participants (unless they chose to disobey instructions, that is). Thus, some other mechanism of increasing RA was required. Instead of preserving the movement plans formed prior to movement onset, participants may instead have solved this problem by preserving memory traces of the proprioceptive feedback they received during movement and the fine adjustments made in response to that feedback. Switching hands meant doing without that information, as the most recent use of the new hand was at least 2 trials previously (and often many more).

In sum, Experiment 1 has produced evidence suggesting that people simultaneously prepare movements before deciding between them, as evident in longer participant RTs for central versus lateral targets. This decision operates on neural competition between representations of movements in different directions. Experiment 1 also showed that repeating the use of a hand affords greater response accuracy than switching hands, and that right-handed people display a slight response bias in favour of their dominant hand. However, Experiment 1 contains a confound: participants were not required to fixate on any point on the screen prior to target presentation, and thus participants may have been moving their eyes to each target from inconsistent starting points. If competition between movement directions is effector-independent, occurring even when the conflicting movements concern separate hands, it stands to reason that it may also occur when the conflicting movements concern separate organs. Furthermore, saccades necessarily redirect spatial attention towards their endpoints (Hoffman & Subramaniam, 1995), meaning that participants may have inadvertently improved or impaired their performance on any given trial by incidentally performing a saccade towards or away from the target location just prior to target onset. Controlling the timing of saccades and addressing the open question of inter-effector competition was the primary motive behind Experiment 2.

3.2 – Experiment 2

In Experiment 2, 19 participants viewed a fixation cross before responding to a target in one of four positions with their choice of hand. The fixation cross could appear in one of two locations on the screen, with one location on the left side of the screen between Targets 1 and 2, and the other location on the right of the screen between Targets 3 and 4. Thus, Targets 2 and 3 could appear to the left or the right of the fixation cross depending upon the cross location. The predictions for this experiment were as follows:

1) Participants were expected to produce responses according to the same pattern as in Experiment 1, with the proportion of right hand responses being lowest for the leftmost target (Target 1) and highest for the rightmost Target (Target 4).

2) MT was also expected to be shorter for ipsilateral versus contralateral responses, for the same reason as in Experiment 1: each target is closer to the ipsilateral hand than it is to the contralateral hand.

3) Participant RT to Targets 2 and 3 was expected to be influenced by fixation cross position. The horizontal lateralization of the cross and target locations meant that on some trials, participants had to move their hand to the target in the same direction that they had to move their eyes, while on other trials they had to move their hand in the opposite direction. Same-direction trials were called “congruent” trials, while opposite-direction trials were called “incongruent” trials.

Of these three predictions, Predictions 1 and 3 were borne out by the results. Two additional results, a faster RT for right hand responses and a more accurate RA for right hand responses, will also be discussed.

The pattern of response choices for Experiment 2 was the same as for Experiment 1; Target 1 produced the lowest proportion of right hand responses, with each successive target producing successively higher proportions (Table 2.2). In other words, the more rightward the target, the more often participants chose a right hand response. This pattern demonstrated a distinctive difference from Experiment 1, however, in that every target produced majority right hand responses, even the two on the left side of the screen. This more extreme bias may be due to an increase in handedness scores amongst the Experiment 2 participants relative to Experiment 1 participants. In Experiment 2, the average score was +91 versus an average score of +69 for Experiment 2, while the minimum score was +69 versus +20. An average score of +91 indicates that very few participants in the experiment reported preferring their left hand for more than one or two tasks; the vast majority of tasks that these participants perform in their daily lives are mostly or exclusively performed with their right hands. The Edinburgh Handedness Inventory is a highly imperfect measure of handedness; the instructions are sometimes confusing and require lengthy explanation to avoid error, few tasks are ever directly relevant to the experimental task, and several tasks appear to either have little stability over time, offer only marginal contributions to participant scores, or have a high covariance and are thus redundant (Bryden, 1977; Dragovic, 2004; McFarland & Anderson, 1980; Veale, 2014). Nevertheless, an average score so close to +100 indicates something that participants in Experiment 2 could probably have explained verbally if they'd been asked the right question: they simply do not use their left hands for anything.

An increased handedness bias in Experiment 2 could also explain the two unpredicted results in this experiment: the faster RT (Figure 2.3) and more accurate RA for right hand responses versus left. If participants in this experiment really do not use their left hands often or at all in their daily lives, then they may have an intrinsic performance disadvantage for left hand actions through disuse, which even the simplicity of the task in Experiment 2 (touch a dot on a screen) could not eradicate. However, this explanation is complicated by the results of the choice condition in Experiment 3, in which neither result reappears. The choice condition is essentially a replication of Experiment 2, with the addition of an irrelevant cue prior to the presentation of the fixation cross and a lengthy “practice session” in the form of the cue condition.

This replication failure occurs in Experiment 3 despite an even more extreme average handedness score (+94) and an even higher minimum score (+71). Of the two additional factors in Experiment 2, the cue condition is more likely to be at fault for the lack of replication. By forcing participants to perform a large number of trials with their left hand to all four targets, the cue condition may have trained away their intrinsic left hand performance disadvantage. Although the task is superficially simple, there are a couple of features of the design which make a trial somewhat unnatural, necessitating a degree of learning before they can be performed both swiftly and accurately; these include the required resting position of the fingers prior to target onset (pressing down on a response pad with each index finger), the requirement that participants keep pressing with their nonresponse hand during the response, as well as the requirement that participants return their hand to it’s precise starting location. None of these task requirements are requirements for touching a small, circular target, such as a button, in real life, meaning that at the start of the experiment participants were most likely performing an action they had never performed before.

One possible objection to this interpretation might be that skill learning is capable of intermanual transfer, in which training on one effector improves performance with another. Although intermanual transfer of skill learning has been demonstrated in numerous contexts such as visual displacement (Imamizu & Shimojo, 1995; Taub & Goldberg, 1973) as well as mirror writing (Bray, 1928; Cook, 1933; Parlow & Kinsbourne, 1989) or other motor sequences (Grafton et al., 2002) under certain learning paradigms, other studies have indicated that transfer does not occur when continuous visual feedback is available (Cohen, 1967; 1973). Since visual feedback was constant in all three experiments and no learning was actually prompted by the task (target presentation was random, and participants did not receive performance feedback), it is unlikely that any intermanual transfer occurred during these experiments. A lack of transfer would explain why Experiment 3, with its higher likelihood of left hand responses, showed no RT or RA hand differences when Experiment 2 did. No RT or RA differences based on hand were detected during Experiment 1 either, where the high degree of lateralization encouraged a greater number of left hand responses than did Experiment's 2 and 3.

The second prediction for Experiment 2, a longer MT, did not come true. The expectation, as per Experiment 1, was that ipsilateral responses would show a faster MT than contralateral responses due to a shorter distance between the starting position and the target. This was not observed; indeed, no MT differences were observed at all. A graph of the data shows a hint of an interaction between position and hand, with left hand MT's faster to Target 1 than right hand MT's but vice versa for Target 2. This interaction is unlikely to be real, as it is difficult to understand why right hand MT would be faster for Target 2 but not Targets 3 or 4, where the distance between response pad and target favours the right hand and where the odds of a right hand response are high. It's also not clear why left hand MT might be faster than right hand MT for Target 1, but not vice versa for Target 4 given that the participants are right handed and thus less likely to require time-consuming error corrections during right hand responses.

The reason for the lack of an MT result depending upon laterality is probably simple: MT increases with distance, and the reduced number of targets and reduced laterality of the target array in Experiment 2 meant that participants never had to reach as far in Experiment 2 as they did in Experiment 1. Experiments 1 and 2 represent a tradeoff: the reduced number of targets in Experiment 2 was intended to increase participants’ willingness to make left hand responses, but doing so meant eliminating the most highly-lateralized targets which evoke the greatest response differences.

The final prediction, that congruent trials would show a faster RT than incongruent trials, was confirmed (Figure 2.4). There are three possible explanations for this difference. The first explanation is that conflicting movement directions between the saccade to the target and the reach to the target on incongruent trials delayed decision-making via competition, just as conflicting movement directions between the left and right hands delayed decision-making for central targets in Experiment 1. The second explanation is that the inconsistent location of the target in retina centered space versus hand centered space during incongruent trials mandated an extra processing step: a reference frame transformation. During congruent trials, targets presented within the right visual field are on the right side of the body and vice versa; during incongruent trials, targets presented within the right visual field are actually on the left side of the body, and vice versa. This incongruency, according to the reference frame explanation, requires a more difficult transformation resulting in a longer RT. This reference frame explanation stands in challenge to the affordance competition hypothesis, which proposes a fundamental blurring of the perceptual, cognitive and motor systems. A reference frame transformation is a classic cognitive function, taking visual information as input and performing computations on it, with results made available to the motor system for execution (Jeannerod, 1995).

The third potential explanation for this result concerns the nature of spatial attention. The fixation cross that preceded each target appeared in one of two locations: between Target 1 and Target 2 on the left side of the screen, and between Target 3 and Target 4 on the right side. This arrangement allowed Targets 2 and 3 to appear within the right visual field or the left depending upon the location of the cross. Trials where the target's screen side and visual field side matched (for example, Target 3 preceded by a left-sided cross were called congruent trials, while non-matching trials (for example, Target 3 preceded by a right-sided cross) were called incongruent trials. However, this arrangement is unfortunately asymmetrical: the distance on the screen between the cross and the target was larger for congruent trials than it was for incongruent trials. Put another way, targets during congruent trials were more highly lateralized within the visual field than targets during incongruent trials. This asymmetry matters because past research has shown that spatial attention is more readily captured by targets appearing in the peripheral visual field than by targets appearing centrally (Posner, 1980; Posner & Cohen, 1984; Remington, 1980).

Experiment 2 (and 3) also bears some similarity to a spatial cueing task. These experiments were not designed as a spatial cueing task, and there are a number of differences between them and a typical version of the task (the fixation cross location was not predictive of the target location, for example). Nevertheless, the presentation of a fixation cross at the outset of each trial functioned as a spatial cue, drawing participants' eyes and attention to that location. Although the visual angle of each participants' locus of attention can't be known within these experiments, it is possible that the incongruent targets, being located closer to the cross location than congruent targets, may have selectively fallen within this attentional locus. If this was the case, then Experiments 2 and 3 were essentially modified spatial cueing tasks, with some targets appearing in cued locations and some targets appearing in uncued locations. Mitigating against this possibility is the fact that response times are typically faster to cued locations versus uncued locations (Eriksen & Hoffman, 1972; Posner, 1980; Posner et al., 1978; 80), and in these two experiments the response times were either slower to the "cued" locations (Experiment 2; Figure 2.4) or identical between "cued" and "uncued" locations (Experiment 3).

Unfortunately, the behavioural data presented in this thesis is not sufficient to differentiate between these three explanations. Experiment 2 (and 3) was conceived and executed as an EEG experiment, and it was expected that differences, or the absence of differences, in an EEG waveform called the LRP between congruent and incongruent trials would differentiate them. Differences in P1 amplitude between congruent and incongruent targets would also shed light on whether the incongruent targets were being attentionally cued by the preceding fixation cross. The EEG data from the experiment is not reported in this thesis, however. Ultimately, what can be concluded from the behavioural data is merely that varying the visual field which a target appears in does make a difference when it comes to RT.

Overall, Experiment 2 has reaffirmed that participants choose left or right hand responses to targets in relation to the laterality of the target, as well as provided novel evidence that varying the visual field that central targets appear in makes a difference when it comes to RT. In Experiment 3, this novel result was tested further by introducing a cued condition in which participants were not free to choose their response.

3.3 – Experiment 3

In Experiment 3, 18 right handed participants performed a cued and a free choice version of Experiment 2. Prior to each trial, a red or blue square was presented. Prior to each block of cued trials, participants were given instructions specifying which hand each colour indicated; prior to each block of choice trials, participants were instructed to ignore the coloured squares and respond with whichever hand they wanted.

Experiment 3 was designed to further test the RT effect from Experiment 2, in which incongruent targets evoked longer RTs than do congruent targets. Two explanations of this effect were proposed:

1) The conflict between the direction of the saccade to the target and the reach to the target requires neural competition to resolve, much as the conflict between the movement direction for the left and right hand in Experiment 1 did.

2) The presentation of a right side target in the left visual field and vice versa requires a difficult reference frame transformation before participants can accurately respond.

The cue condition was expected to resolve this mystery by eliminating competition as a possible explanation. Participants knew which hand they were going to respond with prior to target presentation, and even though a proto-movement plan was likely initiated automatically for the un-cued hand anyway (Bub & Masson, 2010; Masson et al., 2011) the resulting competition would be heavily biased in favour of the cued hand and thus more swiftly resolved. The counterbalancing of the cue colour within the cue condition means that on half of all relevant trials participants are not strongly preparing a response with the contralateral hand, only the ipsilateral hand. With a wider angle between starting position and target, the contralateral hand conflicts more so with saccade direction than does the ipsilateral hand, for which a movement to the target is nearly straight forward. Eliminating the contralateral hand as a movement option therefore removes the primary source of any competition. However, a reference frame transformation is required during incongruent trials no matter which hand participants use or why. If the congruency RT effect arises during the cue condition, then the reference frame explanation is more likely to be correct; if it does not arise, then the competition hypothesis is correct.

The results of Experiment 3 are, unfortunately, somewhat ambiguous. Incongruent trials did not produce longer RTs than congruent trials during the cue condition, as might be expected if the competition hypothesis is correct. However, no congruency effect was detected in the choice condition either. The congruency effect from Experiment 2 did not replicate, therefore no firm conclusions can be drawn about the cause, or even the existence, of the congruency effect. This result does, however, make it more unlikely that the congruency effect was due to any kind of spatial cueing by the fixation cross. Although the introduction of the cue condition did not serve as an adequate control for the congruency effect from Experiment 2, it was still possible to employ it as a control for a different effect: the effect from Experiment 1 whereby central targets produced longer RTs than lateral targets (Figure 2.1). This was the original finding which motivated the introduction of the congruency condition in Experiment 2. Experiment 3 replicated the effect during the choice condition while also suggesting that this effect is exclusive to voluntary actions (Figure 2.6). Central targets actually produced significantly *faster* RTs than lateral targets in the cue condition. Target laterality appears to affect performance regardless of whether an action is voluntary or not, but in very different ways. Although the failure to replicate the congruency effect from Experiment 2 means that the cause of this laterality effect remains elusive, the result itself appears much more robust and meaningful in light of Experiment 3.

Experiment 3 made two minor predictions, one of which was supported and one of which was not. RT was expected to be faster overall during the cue condition than during the choice condition due to the lack of competition between hands. This was not the case, although MT turned out to be faster during the choice condition, a result which has been found before (Becchio et al., 2014). It's possible that the need to remember the cue colour (as well as the instructions from the beginning of the trial block) may have slowed participants down in the cue condition. Instead of having to choose a response hand, participants had to remember the identity of a cue, which may require just as much time to do. Task-relevant info from a cue is maintained during cue-delay-target tasks by a fronto-parietal network (Andersen & Cui, 2009; Dosenbach et al., 2013; Hoshi et al., 2000; MacDonald et al., 2000; Miller & Cohen, 2001), and must be integrated with motor regions in order to guide performance (Cisek & Kalaska, 2010). Alternatively, similar cue-delay-target tasks have previously found that effector-specific information is localized within the same brain regions, the dorsal premotor cortex (PMd) and the posterior parietal cortex (PPC) as spatial information about potential targets (Calton et al., 2002; Cui & Andersen, 2007; Hoshi & Tanji, 2000). Thus, the overall flow of information during movement planning is similar regardless of the order in which movements are specified and selected. However, unlike in the choice condition where these two processes are carried out simultaneously, the temporal dissociation of these processes in the cue condition means that participants must carry out an additional integration process before a movement can be performed. An altered experiment design, in which the cue co-occurs with target presentation, would be able to control for this additional process and determine its impact. This could easily be accomplished by substituting the visual cue for an audio cue, which could then be presented before or with the target, or even after it.

Cued responses were also expected to be more accurate than chosen responses, due to the lack of “noise” in the movement direction caused by preparation of the unused hand, and this result did occur (Figure 2.7). Together, these results in combination with the recurrence of the laterality effect provide moderate evidence that competition occurred during the choice condition but not the cue condition. By extension, this also supports the conclusions of Experiments 1 and 2 that competition occurred.

One final result from Experiment 3 worth mentioning is the observed interaction between hand use and target position on RT within the cue condition. Participants were faster to respond to left-sided targets with their left hand and vice versa (Figure 2.5). This was not found within the choice condition, nor was it found in Experiments 1 and 2, which consisted entirely of “choice” responses. In fact, in Experiments 1 and 2 the interaction was the opposite, especially for the two most lateralized targets. The ipsilateral RT effect in the cue condition is most likely related to anticipatory preparation of the ipsilateral hand caused by the colour cue interacting with the lateralized positions of the fixation cross. Although cross location did not predict target location, it nevertheless would have cued participants’ attention to that location, and past experiments have shown that cueing a person’s attention to one side of space typically results in faster response times to targets when ipsilateral responses are instructed, even when the cue is unpredictive of target side (Simon, 1990; Simon & Berbaum, 1990; Simon & Rudell, 1967; Simon

& Small, 1969). This effect didn’t occur during the choice condition (or during Experiments 1 and 2) because this effect occurs when responses are instructed, and the choice condition allowed participants to disregard the cue and choose their own response hand.

Overall, the different patterns of performance for voluntary and non-voluntary actions in Experiment 3 supports the conclusion of Becchio et al. (2014) and others (Cunnington et al., 2006; Filevitch et al., 2013; Goldberg, 1985; Lau et al., 2004, 2006; Thaler et al., 1995) that voluntary and non-voluntary actions are kinematically and neutrally distinct.

3.4 – Summary

The three experiments reported in this thesis comprise an attempt to elicit and measure response competition in humans using a simple task not much different from pushing a button in real life. Competition has been demonstrated in humans before, but only on cued tasks where the potential response options all involve the same effector (Chapman et al., 2010; Gallivan et al., 2015; 2016; Praamstra et al., 2009). The world outside of the lab rarely limits one’s interaction with it to a single effector, however; most of the time, people are free to choose the effector they want to use, and it is important to investigate the processes by which people make this choice. From these three experiments, two consistent findings emerged. First, when presented with spatially lateralized targets and given the opportunity to choose their response hand, participants typically scale their choices to the degree of lateralization. The further to their left a target appears, the more likely they are to use their left hand, and vice versa. Second, when targets are presented near their midline, participants take longer to produce a response than they do when targets are presented further to the side. This is likely because they are producing movement plans for each hand which must then compete with each other to determine a response. In Experiment 3, participants demonstrated that these volitional actions are behaviourally dissimilar from stimulus-driven actions. Volitional responses are slower to central targets while stimulus-driven actions are actually slower to lateralized targets, indicating that the impact of increased competition on response times is probably quite large. Furthermore, volitional actions are generally performed less accurately than stimulus-driven actions, possibly due to noise introduced into the “winning” movement plan by the losing plan.

Each experiment in this thesis possesses limitations, which ought to be considered in order to avoid misinterpretation of the results. In Experiment 1, participants were not presented with a fixation point prior to target onset. This means that, while the direction and the extent of participants’ hand movements from the response pad to the screen were consistent across trials and between participants, the direction and extent of their saccades to the target were likely not. On different trials, the same target position could have appeared to the participants in different regions of visual space depending upon where they had been resting their gaze prior to target onset. This is a problem, because past research has shown that different regions of space attract attention in unequal ways (Handy et al., 2003). Additionally, saccades made just prior to target onset may have inadvertently improved or impaired performance depending upon whether the saccade was towards or away from the target location (Hoffman & Subramaniam, 1995). To resolve these problems, Experiment 2 introduced a fixation cross prior to target onset, and the placement of the cross on either the left side of the screen or the right side in Experiment 2 allowed not just for the control of saccade direction, but also their manipulation.

The design of Experiment 3 also had a particular limitation, in that participants always performed blocks of cued trials prior to blocks of choice trials. This was primarily done because in Experiment 2, which shared the same fixation cross and target locations as Experiment 3, some participants produced very few or no left hand responses to contralateral targets, resulting in analysis difficulties. It was hoped that the experience of performing such movements during the cued condition would encourage participants to view them as an available option during the choice condition, and the results showed that this was effective. However, the lack of condition counterbalancing does mean that participants performed the choice condition trials with greater experience, and possibly fatigue, than they did in the cue condition trials. Although it wasn't formally documented, several Experiment 3 participants did express fatigue at the number of movements they were asked to perform following the conclusion of the experiment, and if this fatigue affected their performance at all it would have done so during the choice condition.

Finally, all three experiments suffer from a shared limitation, which concerns the generalizability of the results rather than their validity. Although the task of choosing a response hand has a great deal of ecological validity, the targets that were presented do not. In each experiment, the target was a small, black circle on a white screen, which resembles no interface that people are likely to encounter outside of the lab. These targets are of similar size and shape to several familiar objects, such as an elevator button or a doorbell, but unlike those real-world objects the targets have no texture and offer no feedback, and although the targets do have a boundary they don't have an edge. When people press an elevator button it depresses in order to close the circuit and instruct the elevator, and their movement plans must account for this depression if they are to complete the action successfully. Another difference is that, if people accidentally press the edge of an elevator button rather than the center, they can feel that they've done so. When it comes to the targets, however, touching the center of the target felt exactly the same as touching the boundary between it and the rest of the screen, and the same as missing it altogether. Therefore, while the movements that participants performed should resemble movements in the real world during their initial and middle phases, the end-stage of the movement where participants prepare for contact is probably unique to the experiment. The targets in these experiments, being mere images on a computer screen, required participants to terminate their forward movement on contact, and therefore the actions performed in these experiments are not fully comparable to such real-world actions, despite the targets' visual similarity to several real-world objects. Touch screens have recently become extremely common with the commercial availability of smartphones and tablets, however, and the displays that people interact with are usually much more complex than the displays in these experiments, while also requiring greater precision. It's very likely, therefore, that no participant was interacting with a touch screen for the first time, and many participants likely had extensive touch screen experience. Nevertheless, the movement time and accuracy data should be considered in light of the differences between the task and comparable real-world actions.

Taken together, these three experiments provide evidence that response competition operates on movement direction and is at least partly effector-independent, occurring even when potential response options involve different effectors. These response preparations occur prior to action selection and are fundamental to how humans and other complex organisms behave flexibly and intelligently in a world full of choices (Cisek & Kalaska, 2010; Gibson, 1979). Future investigations of this topic are already in progress. All three experiments were performed while participants underwent EEG, and analysis of that data ought to substantially refine the results reported here. In particular, analysis of the lateralized readiness potential (LRP), which reflects the difference in activity between the left and right cortical hemispheres during unimanual actions, is expected to spotlight the presence and degree of neural competition occurring to each target within the three experiments. In Experiments 2 and 3, a larger LRP for congruent trials versus incongruent trials would significantly strengthen the notion that neural competition is a factor during these trials. An analysis of the P1 ERP might also reveal whether spatial attention is variably allocated across the visual field during simple reach tasks, while a comparison of the P1 and the LRP would contribute to further understanding of how spatial attention facilitates actions. A fourth experiment in this series, in which visually-guided actions are contrasted against memory-guided actions, is also underway. Memory-guided actions are neurally and behaviourally distinct from visually-guided actions, but the extent to which these differences are a factor during motor competition is currently unknown.

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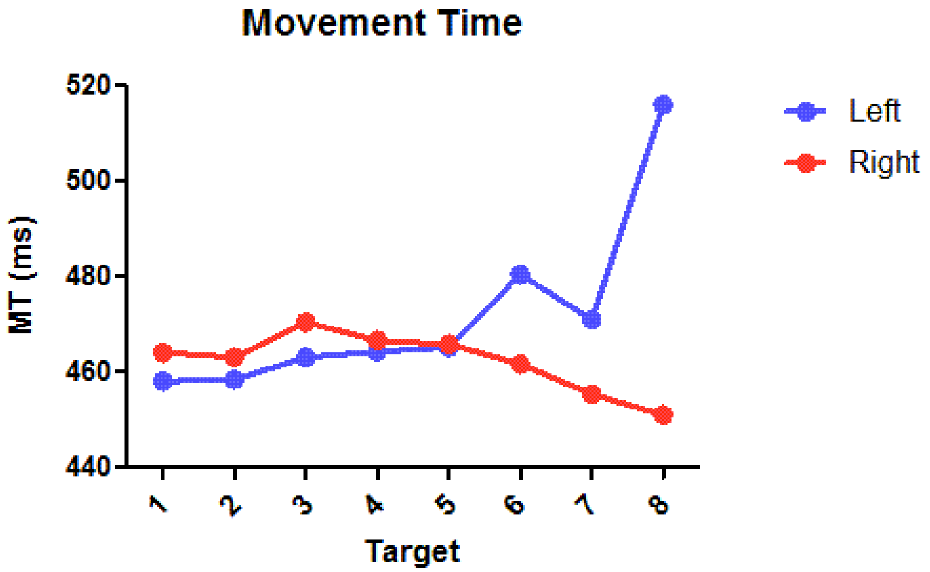
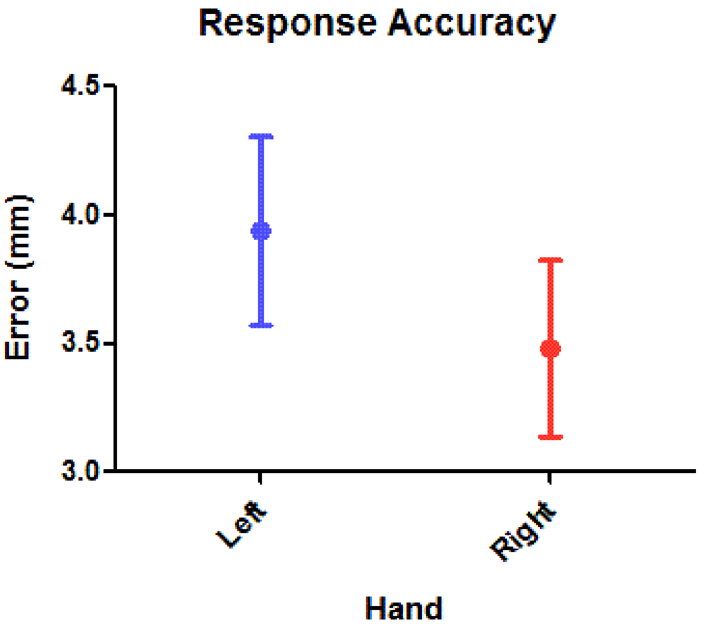
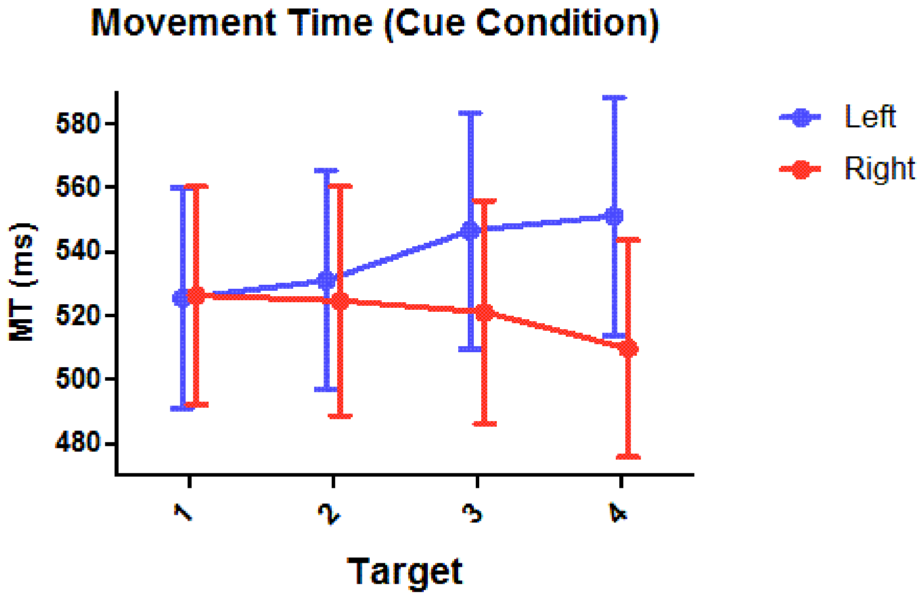
Appendix



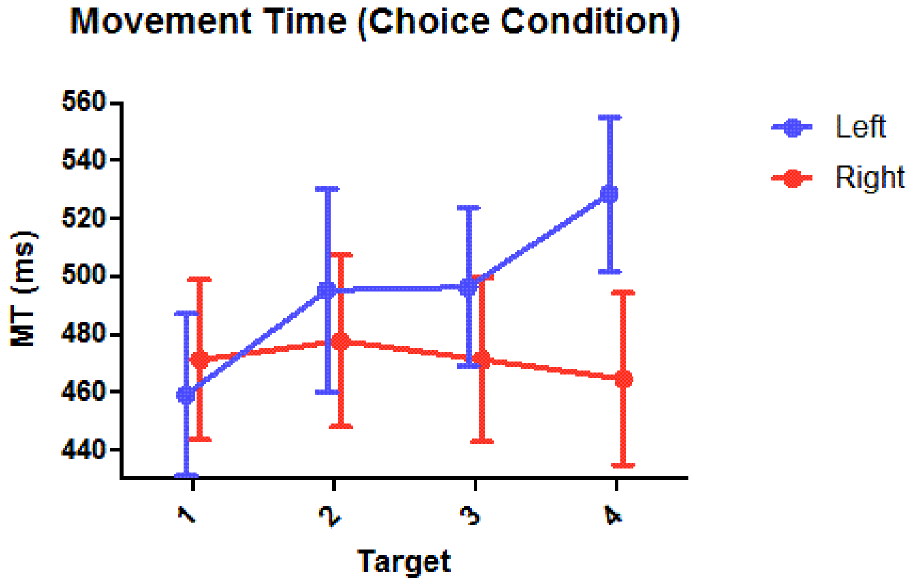
Appendix A – Movement times for the left and right hand at each target position in Experiment 1. An interaction was observed between hand use and target position (p = 0.017), meaning that left hand MT was faster for left-sided targets than right-sided targets while right hand MT was faster for right-sided targets than left-sided targets.



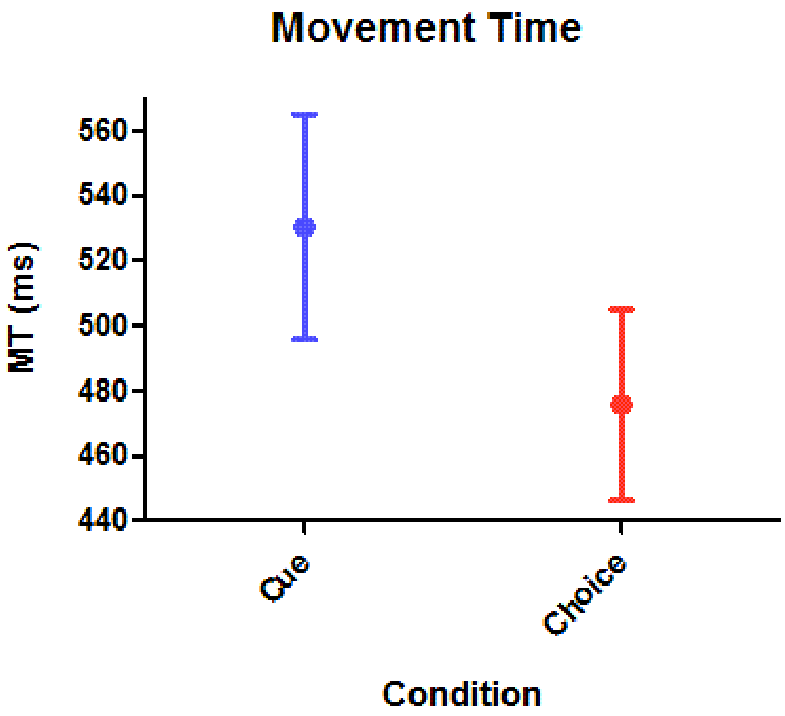
Appendix B – Response accuracy for the left and right hand in Experiment 2. Responses were significantly more accurate when performed with the right hand regardless of target position (p = 0.032).



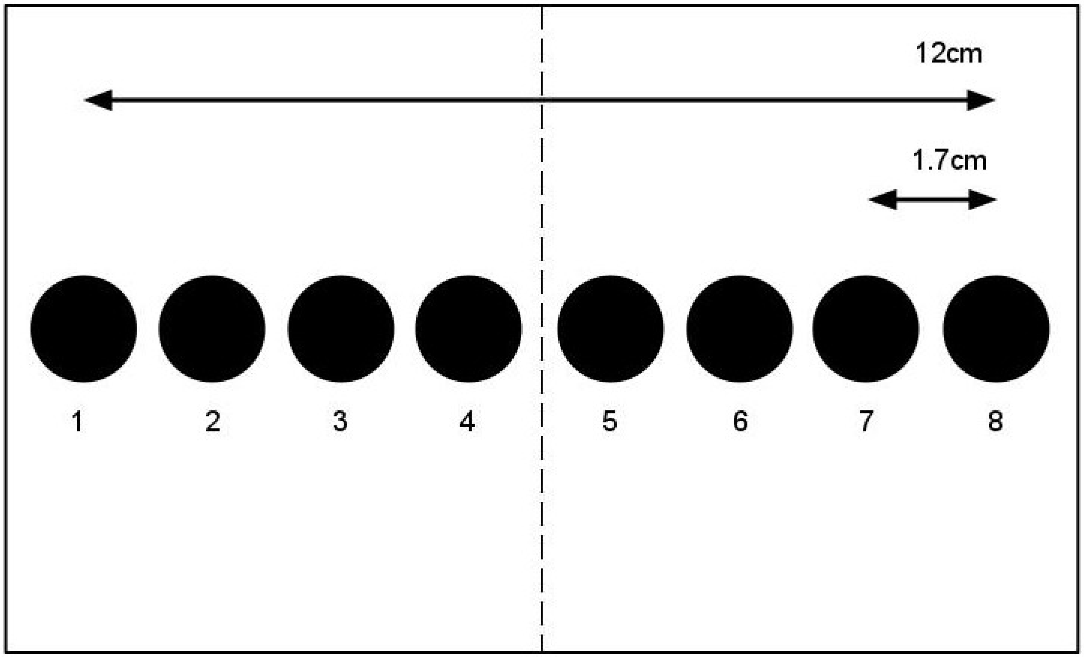
Appendix C – Movement times for the left and right hand during the cue condition in Experiment 3. An interaction was observed between hand use and target position (p < 0.001). As the target was shifted from left to right, right hand MT became faster but left hand MT became slower.



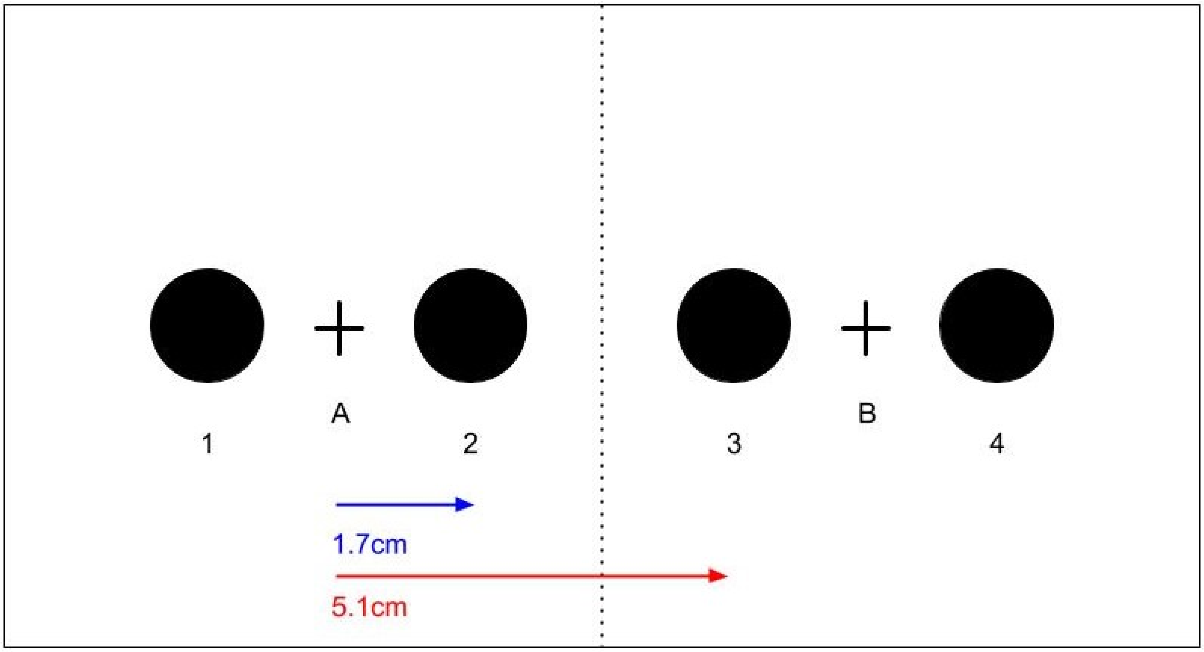
Appendix D – Movement times for the left and right hand during the choice condition in Experiment 3. Main effects of hand (p = 0.031) and position (p = 0.034) were observed, as was an interaction (p = 0.012). Right hand MT was faster than left hand MT and MT was faster for left-sided targets than right-sided targets, while rightward shifts of the target produced generally faster MTs for the right hand but slower MTs for the left hand.



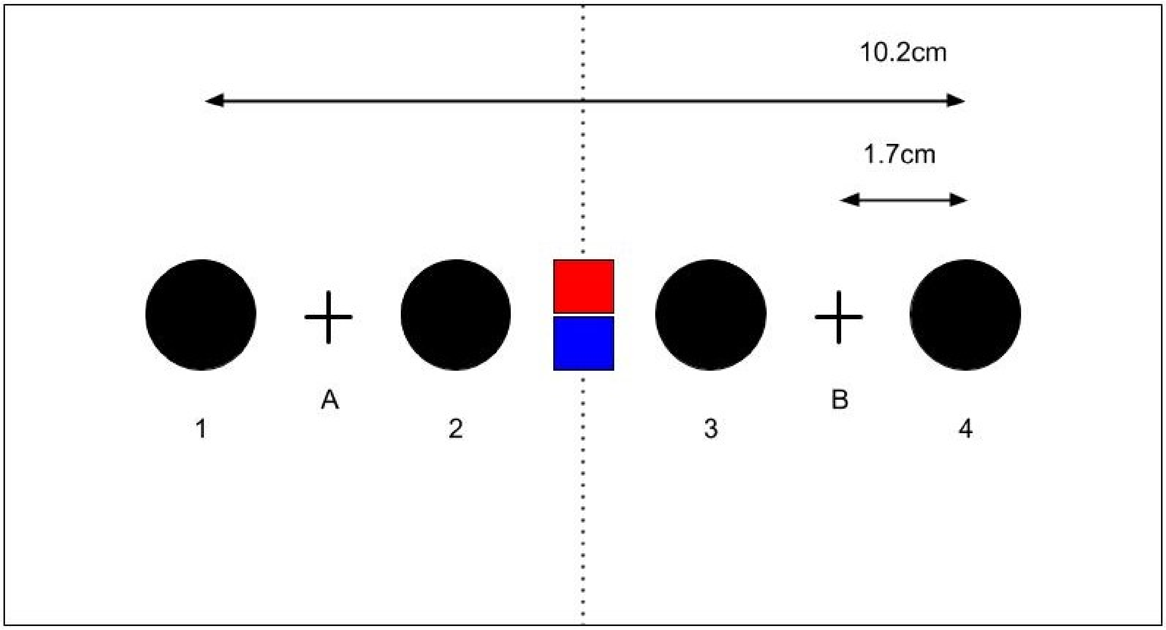
Appendix E – Movement times for central targets during the cue condition and the choice condition in Experiment 3. MT was significantly faster in the choice condition than the cue condition (p = 0.036)



Appendix F – Experiment 1 paradigm. On each trial, a single target was presented in one of 8 lateralized positions. Target sizes are not to scale.



Appendix G – Experiment 2 paradigm. On each trial a fixation cross was presented in one of two lateralized positions, followed by a target in one of four lateralized positions. Trials involving Target 2 or Target 3 were categorized as either Congruent or Incongruent. On Congruent trials, the visual field that the target appeared in matched the target's screen side (Ex. an A3 trial). On Incongruent trials, the visual field did not match the screen side (Ex. An A2 trial). Cross and target sizes are not to scale.



Appendix H – Experiment 3 paradigm. On each trial a red or blue colour cue was presented, followed by a fixation cross and then a target. Trials were divided into two conditions, a Cue Condition and a Choice Condition. During the Cue Condition, each block of trials was preceded by instructions identifying which colour cued which response hand. During the Choice Condition, participants were instructed to ignore the cue and choose their own response hand. Cue, cross, and target sizes are not to scale.