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READY FOR ACTION: FIXATIONAL LIMB MOVEMENTS

REVEAL FORTHCOMING VOLUNTARY MOVEMENTS

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Rajal G. Cohen

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The dissertation of Rajal G. Cohen was reviewed and approved* by the following:

David A. Rosenbaum
Distinguished Professor of Psychology
Dissertation Adviser
Chair of Committee

Dagmar Sternad
Professor of Kinesiology
Minor Adviser

Paola Giuli Dussias
Associate Professor of Spanish, Linguistics and Psychology

Cathleen M. Moore
Adjunct Professor of Psychology

Daniel J. Weiss
Assistant Professor of Psychology

Melvin M. Mark
Professor of Psychology
Head of the Department of Psychology

*Signatures are on file in the Graduate School.

ABSTRACT

Physiological indices of cognitive processes have been the focus of considerable interest. They can be found in brain activity, facial expressions, microsaccades, and neck muscle activation. Recent work suggests that they also occur in fixational limb movements, which may include drift, tremor, and small quick movements. In the studies reported here, limb movement was measured while participants pointed to a central location and anticipated a target-directed movement. During the pauses before voluntary movement, the amplitude of small "fixational" movement increased in the axis of forthcoming target-directed movement relative to the orthogonal axis, while frequency decreased in the axis of forthcoming target-directed movement relative to the orthogonal axis. These fixational movement biases may be online indicators of attention or some other cognitive process. Alternatively or additionally, they may reflect some functional aspect of motor preparation. This project investigates the phenomenon of fixational limb movement biases and seeks to elucidate whether, and in what manner, they reflect mental and physiological aspects of readiness.

In Experiments 1-3, participants memorized and then performed simple sequences of pointing movements that included long pauses. Experiment 1 verified that the effects held across different limb segments, and Experiments 2 and 3 confirmed that they were robust to various exploratory manipulations, including changes in instruction mode, internal vs. external timing, and pause duration. The amplitude effect depended on the proportion of recent movements made in each axis, suggesting that fatigue and gravity might play a role. Analysis of results with and without the last submove indicated that the countermove was critical to the frequency effect. Furthermore, when the last submove was removed from the period of analysis, vision was critical to the amplitude effect.

In Experiments 4-6, participants responded to cues. Cue validity had a large influence on the effects. Discreteness or reciprocity of the movement and size of the staging area had smaller influences. The influence of the size of the staging area provided support for the hypothesis that the effects are due at least in part to participants drifting toward the expected target and correcting. Additional analyses provided support for the idea that for rapid discrete movements with known start times, fixational movements in advance of movement onset promote synchronization of discrete movement onset with ongoing oscillation. Finally, correlations of effects with performance suggested that the countermove had a facilitatory effect on movement times.

In sum, the dependency of fixational limb movements on the direction of intended or expected forthcoming movement most likely has several sources. Support was found for: (1) the countermove, which serves to build up elastic energy immediately before the voluntary movement; (2) engagement of attention by the direction of forthcoming movement, combined with effort to maintain position with respect to a visual cue; (3) synchronization of fixational movements with respect to the expected time and direction of discrete movement onset. Other plausible relations between fixational and voluntary movements are discussed.

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CHAPTER 1
INTRODUCTION
Readiness

Readiness is a psychological state that includes a cognitive representation of some expected stimulus, some intended action, and some intended result. While cognitive representations cannot be directly measured, shorter reaction times are generally taken as evidence for heightened readiness (Posner, Snyder & Davidson, 1980; Wundt, 1874 (cited in James, 1890, p. 428). In addition, every psychological state has physiological correlates. The physiological correlates of readiness are known to include changing patterns of electrical activity in the brain (Kornhuber & Deecke, 1965), lowered reflex thresholds (Gurfinkel & Kots, 1966), and increased muscle tone (Sherrington,1906).

This first section of the introduction will discuss each of these indices turn. The second section will review the literature investigating the relation between small movements and cognition, ending with a description of a new window into readiness, which relies on biases in the small movements made while one is ostensibly holding still. I call these *fixational movements*. The third section reviews previous literature relating fixational movements to voluntary movement. The fourth section introduces hypotheses to be tested.

Reaction Times

In a reaction time tasks, responses are faster to stimuli that are preceded by warning signals than to stimuli that are not (Wundt, 1874, cited in James 1890). Response preparedness can be assessed by varying the time between a warning signal and a go stimulus and comparing the resulting reaction times. Evidence suggests that general response readiness builds up gradually over 300 ms, is maintained for about 400 ms, and then gradually fades (Gottsdanker, 1975).

In addition to general readiness to respond, there is also the possibility of specific readiness to make particular responses. One way such specific readiness has been explored is with the now classic cuing task of Posner, Snyder, and Davidson (1980). Here, participants receive preliminary information about the likely location of a peripheral stimulus. When the stimulus arrives, they respond as quickly as possible. When the preliminary information (the cue) correctly indicates the target direction, the cue is considered valid, and when the cue indicates the wrong direction it is considered invalid. Typically, responses are fastest when the cue is valid and slowest when the cue is invalid. This *validity effect* demonstrates that participants prepare for the peripheral stimulus to appear in the expected location. Hundreds of variations on this task have affirmed the robustness of this effect and refined the conclusions that can be drawn with the method. For a review, see Hackley & Valle-Inclán (2003).

Brain Activity

Electrophysiological methods allow researchers to investigate readiness in the brain, and to distinguish preparation for a self-generated movement from readiness to respond to a cue. Beginning up to 1500 ms before the initiation of self-generated movements, electroencephalography (EEG) reveals activity in the supplemental motor area of the cortex. This activity is known as the readiness potential, or *Bereitschaftspotential* (Kornhuber & Deecke,

1965, cited in Brunia & van Boxtel, 2001). The readiness potential is not found for movements that are externally cued (Deecke, Scheid, & Kornhuber, 1969). However, another wave of electrical activity, called the *contingent negative variation*, is found over much of the frontal, central and parietal cortices, beginning up to 1000 ms before an externally cued movement (Walter et al, 1964). These results suggest that readiness to initiate movement has a corresponding brain state, and readiness to respond to an expected cue has a different corresponding brain state.

Direct observation of the brain also reveals information about aspects of preparation for specific movements. For instance, recordings from neurons in the motor cortex of monkeys reveal different patterns of activity depending on the direction of the forthcoming movement (Georgopoulos, Schwartz, & Kettner, 1986). Some of these neurons reflect direction of movement in arm-centered coordinates, whereas others reflect direction of movement in extrinsic space (Kakei, Hoffman, & Strick, 1999). In addition, direct stimulation studies (also performed in monkeys) suggest that some motor neurons code not for movement but for posture (Graziano, Taylor & Moore, 2002). Farther "upstream" in the brain, neurons reflect progressively more abstract features of movement (Kakei, Hoffman, & Strick, 2001). Presumably, preparation in the brain involves progressive translation from abstract and world-centered representations to commands that can be physiologically implemented.

Changes in Reflexes

Some early observations about motor preparation were made by James (1890) and Sherrington (1906), who both described a general increase in muscle tone during preparation for movement. A change in tone may be caused by decreasing reflex thresholds of gamma neurons. Prochazka (1989) suggested that sensorimotor gain is adjusted by the CNS according to the predicted demands of the situation in which an organism finds itself. Sensorimotor gain is set higher for conditions of high arousal, novelty, or difficulty, and lower for familiar movements in familiar contexts. In support of this idea, there is evidence that reflexes become more sensitive during movement anticipation. Scheirs and Brunia (1985) found sustained augmentation of both tendon reflexes and stretch reflexes for up to 4 seconds after a warning signal that was to be followed by movement. This is an example of global tuning of reflexes.

In addition to a general change in reflex settings, researchers have shown that reflex thresholds may be specific to the forthcoming action. When a tendon is quickly stretched, as when a doctor taps a knee, stretch receptors in nearby muscles activate a sensory nerve. The sensory nerve sends a signal to the spinal cord, where it activates a motor nerve, which sends a signal back to the muscle, resulting in a quick kick. This series of events is known as a tendon (T-) reflex. To study these reflexes in the laboratory, researchers create a variation called the Hoffman (H-) reflex. They bypass the tendon and muscle by electrically stimulating the sensory nerve. The resulting muscle activity can then be measured. In an experiment by Gurfinkel & Kots (1966, cited in Prochazka, 1989), participants heard a warning tone followed by a signal to move. When the H-reflex was triggered during the interval between the warning signal and the subsequent go signal, it was stronger than when it was triggered without a warning signal. The increase was greatest in the muscles that were going to be primarily responsible for the upcoming movement. Thus, the central nervous system was preparing specifically for movement in an expected direction by altering reflex sensitivity accordingly. Another study demonstrated than when

participants were to merely *imagine* moving a leg, reflexes were amplified more in the leg that participants had been asked to imagine using than in the contralateral leg (Bonnet, Decety, Jeannerod, & Requin, 1997). The preceding examples all refer to the tuning of short-latency reflexes. There is also evidence for tuning of long-latency reflexes. Koshland and Hasan (2000) had participants execute fast arm movements to a target. They found that when participants' limbs were perturbed prior to movement, long-loop reflexes responded such that movement in the intended direction was initiated more quickly and with greater force, regardless of the direction of the perturbation. Thus, the tuning of both long and short latency reflexes is sensitive to the direction of intended movement.

Small Movements as Windows Into the Mind

Kinesthetic Illusions and Ideomotor Phenomena

The history of the scientific study of small movements has an unlikely beginning in the study of occult phenomena. In the mid-19th century, there was a great deal of interest in communicating with the dead, and various devices were thought to facilitate this process. One such device was a weighted pendulum. While holding in his or her hand a string with a weight at the bottom, a person would ask yes/no questions and read the answers in the axis in which the pendulum swung. Chevreul demonstrated that the swinging of the pendulum decreased when the arm of the person holding it was externally supported, indicating that the movement was caused by muscular activity. He further demonstrated that the oscillations decreased when the eyes of the person holding the pendulum were closed (Chevreul, 1833, cited in Easton & Shor, 1976). Since the person causing the movement was not aware of initiating it, Chevreul described the pendulum effect as a kinesthetic illusion.

Easton and Shor (1976) discovered that the effect was enhanced if the participant was instructed to focus on the movement and reduced if the participant was instructed to focus on the hand remaining still. The effect was also reduced if participants were required to perform arithmetic while holding the pendulum. Thus, the effect apparently relies on attention.

Wegner, Ansfield and Pilloff (1998) added a twist to the pendulum illusion by instructing participants to *prevent* movement in one axis. They found that the number of direction reversals was greater in the axis of forbidden movement than in the orthogonal axis, and they described this as an "ironic effect," caused by error monitoring. However, they did not report whether the amplitudes of the movements were also larger in the forbidden axis, making their claim difficult to evaluate.

Another supposed means of communicating with the dead was the Ouija board. This, too, was found to be sensitive to small unconscious movements initiated by the user. Carpenter (1852) coined the phrase *ideomotor* to refer to the idea that every thought – conscious or not – has a commensurate action. The ideomotor principle was later popularized by James (1890), fell out of favor during the behaviorist heyday (Thorndike, 1913), and was revived relatively recently (Greenwald, 1970). In a Ouija-board-like experiment, Gordon and Rosenbaum (1984) demonstrated that people could move more slowly when instructed to imagine that they were

being passively moved than when they simply tried to move as slowly as possible. They proposed that under the instruction to allow passive movement, participants allowed movement that was below the sensory threshold. This fits with Chevreul's idea of a kinesthetic illusion.

Micro-expressions

While communicating with the dead is not a topic of great interest to most psychologists, the idea that people make small unaware movements that give away their thoughts is of great interest. One modern example is *microexpressions*: fleeting (less than 40 ms) expressions on a person's face that precede other (often more socially acceptable) expressions. Data suggest that these are predictive of behavior and may be useful for detecting deceit. People trained to attend to microexpressions are better at detecting deceit than people without such training (Ekman & O'Sullivan, 1991; Porter & ten Brinke, 2008). In addition, a neural network trained to identify microexpressions was able to detect deception at a level significantly above chance (Rothwell, Bandar, O'Shea, & McLean, 2006).

Fixational Movements

Another new window into cognition is the movement occurring during periods of intended stillness or fixation. These *fixational movements* can be found in multiple motor systems, including the eye and the arm. When the eye is fixated on a target, very small movements occur. These movements are thought to prevent retinal fading. Three categories of fixational eye movements have been identified (Ciuffreda & Tannen, 1995): ocular drift is slow and is thought to be random in direction; ocular tremor is rapid and oscillatory; and microsaccades are rapid and irregular. Kinematically, microsaccades resemble miniature (less than one degree of visual angle) saccades, and they tend to occur approximately once per second during ocular fixation.

Recently, the bias in microsaccades before movement has been the focus of considerable interest. In the several hundreds ms after a visual cue is presented, the likelihood of a microsaccade occurring in the direction of that cue first increases and then decreases (Laubrock, Engbert & Kliegl, 2005). This has been interpreted as evidence that microsaccades reflect the orientation of attention (Hafed & Clark, 2002; Laubrock, Engbert & Kliegl, 2007). When the target first appears or is indicated, attention is drawn in that direction, a movement is prepared and held waiting, and small failures of inhibition lead to small eye movements in the direction of the forthcoming move. The increase in eye movements away from the target later in the waiting interval may be a result of corrections erroneously made to movements that were successfully inhibited.

Fixational movements can also be found in the arm. When the arm is held in a fixed position, as it is when a person attempts to steadily point at a target, small movements are present and may have several sources. One is postural tremor, which is oscillatory and has components ranging from 2-4 Hz up to 10 Hz, or higher for small limb segments. Another is drift, which is fairly slow and not oscillatory. A third is another type of fixational limb movement analogous to microsaccades for which there is so far scant evidence. Cohen and Rosenbaum (2007) found that when participants pointed to a central target and waited to initiate a movement to a peripheral

target in a known direction, there was an increase in amplitude and a decrease in frequency in the last 500 ms before movement onset along the axis of forthcoming movement. This bias may be an indicator of attention or some other cognitive process. Alternatively or additionally, it may reflect some functional aspect of motor preparation. The project reported here investigates the phenomenon of bias in fixational limb movements and seeks to elucidate whether, and in what manner, this bias reflects psychological and physiological aspects of readiness.

Importance of Fixational Movements

The relevance of small movements as a window into cognitive processes goes beyond mind-reading. It also bears on an important dialogue whose roots go back to the beginning of psychology. The question has to do with the degree of separation between thought and action. While the question is complex, it can be simplified to two opposite perspectives. One is the discrete perspective, advocated by Donders (1868), Sternberg (1969), and Sanders (1990), which proposes that the cognitive system operates in a linear fashion, such that one stage of processing must be completed before the output of that stage is passed on to the next stage of processing, including the response execution stage. The other is the continuous perspective, advocated by James (1890), McClelland (1979), Greenwald (1970) and Prinz (1987, 1997), which proposes that the cognitive system operates in a parallel fashion, such that information in various stages of completion flows continuously. The merits of each proposal have been thoroughly debated (Delong, 1990; Elsner et al, 2002; Fuchs, Kaneko, & Scudder, 1985; Miller, 1988; Requin & Riehle, 1995).

Although the last several decades have seen a gradual erosion of support for pure stage models for early stages of processing, some researchers have suggested that stage models are appropriate for the last stages, where responses are chosen and executed (Gottsdanker & Shragg, 1985; Gazzaniga, Ivry & Mangun, 1998). The study of small fixational movements may contribute to this discussion because, relative to button presses, which are the mainstay of traditional psychology laboratories, small fixational movements occur over a longer period time and so may reveal online processing and incomplete thoughts. If cognitive and neural information flow continuously all the way through to the motor system, one should see such continuous through-put in small fixational movements.

Relations Between Fixational and Voluntary Movements

Regarding possible links between fixational movement and voluntary movement, two lines of research have previously been investigated. Both of these lines of research address tremor but could be applicable to fixational movements more broadly. The first section below reviews the origins of physiological tremor. The second section describes research that considers fixational movements (especially tremor) as a problem and asks whether they can be minimized in certain circumstances, in order to enhance performance. The third section describes research investigating whether the initiation of voluntary movements is timed so as to synchronize with fixational movements (particularly tremor).

Physiological Tremor

The outstretched hand of a neurologically normal person oscillates slightly. This phenomenon, called *physiological tremor*, has been studied extensively since the 19th century by researchers interested in posture and motor disorders (e.g., Herringham, 1890), and its origins continue to be debated (e.g., Morrison & Newell, 2000; Raethjen et al, 2000). Tremor almost certainly has both central and peripheral origins, although researchers disagree about the roles, prevalence, and importance of each. Central tremor arises from oscillators in the central nervous system (CNS) and is most commonly reported in the 10 Hz range. There are numerous sources of 10 Hz activity in the CNS, including specific brain regions and circuits. Which of these are sources of physiological tremor has not yet been definitively established. A likely candidate is the ventrolateral area of thalamus, whose partial removal interrupts both Parkinsonian tremor and physiological tremor (Duval et al, 2000). Purkinje cells in the inferior olive of the cerebellum have also been implicated, but their contribution is debated (Keating &Thach, 1995).

Peripheral tremor arises when some external or internal source of movement (such as the heartbeat or the coincidental synchronous firing of motor units) is filtered by the physical system of the limb (Stiles & Randall, 1967). The frequency and amplitude of peripheral tremor depend on a limb's resonant frequency, which is determined by mechanical properties of the limb such as size, mass, and stiffness. Large limb segments typically have lower resonant frequencies and larger amplitudes than small limb segments. In a healthy adult of average size, the peripheral component of tremor is approximately 25 Hz in the finger (Stiles & Randall, 1967), about 10 Hz and 6 Hz in the hand and forearm, respectively (Marsden, 1984), and about 2 Hz in the shoulder (McCauley & Marsden, 2000).

Of the factors determining of the resonant frequency of a limb, stiffness is the one that can be modified internally. The way this works rests on the similarity of muscles to springs (e.g., Levin & Feldman, 1994) and on the nature of stretch reflexes, which act to quickly correct deviations in posture (Hagbarth & Young, 1979). When a spring is stretched, it resists that stretch. Hooke's Law states that the greater the stiffness of the spring, the greater its resistance for each unit of distance stretched, and thus the more quickly it will return the limb segment back in the direction it came from (Hooke, 1676). Increased stiffness in limb segments may be caused by increased muscle coactivation or by increased gain in the stretch reflexes, either of which tends to lead to an increase in the limb segment's resonant frequency (Stiles & Randall, 1967).

Besides classifying tremor in terms of whether it is central or peripheral, researchers typically consider the context in which it occurs. There are three commonly used contextually defined categories: *resting tremor*, *intention tremor*, and *postural tremor*. Resting tremor occurs in a limb that is relaxed and supported. Intention tremor occurs in a limb when one attempts to initiate a movement. Both of these types of tremor are primarily associated with pathologies. Postural tremor, the main component of physiological tremor, occurs in healthy people, in a limb that is unsupported and unmoving. This is the tremor most likely to contribute to the fixational movements described in this project.

Fixational Movements as a Problem for Voluntary Movement

Studies of fixational movement in healthy people have mostly aimed to reduce its negative effects on tasks requiring extremely fine motor precision. Shooting is one example. Arutyunyan, Gurfinkel, & Mirskii (1968) found that experienced sharpshooters can reduce fixational movements in the hand holding the gun by allowing more freedom in the more proximal limb segments. This allows functional covariation among the movement at different joints, which cancels out the effects on the end-effector. Expert shooters also demonstrate a reduction of heart rate and skin conductance right before shooting, both of which rebound immediately after the shot (Tremayne & Barry, 2001). It has been suggested that rather than gaining skill at suppressing fixational movement, expert shooters learn to be more observant of the waxing and waning of their heart rate, tremor, and other sources of unwanted movement, and to shoot when they are most stable (Morrison, personal communication, 2006).

Another task in which fixational movements can have a negative effect on results is the performance of surgery (Humayun et al, 1997). Biomedical engineers have attempted to develop robotic assistive devices to filter unwanted movement out of the movements of surgeons. However, this is made difficult by the kinematic equivalence of fixational and voluntary movement. Because the devices cannot tell online whether a particular movement is voluntary or not, they tend to function by filtering out all fast movement, and the result is a very slow surgery: useful for novices, but not very practical in the long run (Snyder, personal communication, 2008). Luckily, experienced surgeons, like experienced sharpshooters, can learn to manage their fixational movements constructively. Rooks, Slappery & Zusmanis (1993) showed that experienced surgeons were able to take advantage of high magnification (enhanced visual feedback) to reduce their fixational movements and perform with greater accuracy.

The studies discussed above referred to experts with many years of experience in a task-relevant, high stakes situation. A study of novices found quite different results. Morrison & Keough (2001) asked participants to point to targets and hold as still as possible. When enhanced feedback was provided, the amplitude of fixational movement increased, such that participants were significantly worse at holding still than when no enhanced feedback was provided. This result echoes what Wegner et al (1998) called *ironic mental effects*. Wegner et al found that when participants were instructed to prevent a pendulum from moving in a particular axis, the pendulum reversed directions more frequently in that axis than in the orthogonal axis. They postulated that participants were monitoring carefully for movements in the forbidden axis, and that this monitoring involved visualizing movement in that axis, which leaked and became actual movement in that axis. Thus, while the negative effects of fixational movements on voluntary movement can sometimes be managed, this seems to require extensive practice.

Another way that small movement can have a negative effect on performance is by causing slow cumulative drift away from a desired position. In this case, the negative effect may not be immediately apparent (as is the effect of tremor on shooting a gun), but may be slow and insidious. For example, a music teacher may instruct a pupil to use a particular hand or body position, and the pupil will attempt to comply. However, the pupil may not realize that over the course of a few minutes he or she has drifted away from the instructed position. This kind of drifting can be remediated with constant attention to visual or tactile feedback during extended practice.

Movement Onset Synchronizes With Tremor

Studies of fixational movement in healthy people have mostly aimed to reduce its negative effects on tasks requiring extremely fine motor precision, as described above. However, it is possible that for other kinds of motor tasks, fixational movements serve a useful function for posture, movement, or both. There are numerous ways fixational movements could assist voluntary movement. One that has been considered is the synchronization of movement onset to coincide with tremor phase. With the right timing, it is easier to move an oscillating system than a static one. Thus, if movement onset were synchronized with tremor phase, it might be achieved with less energy. In support of this idea, Travis (1929) found that rapid voluntary flexions and extensions of the forefinger often coincided with the flexion and extension phases, respectively, of 8-12 Hz tremor. Lansing (1957) replicated this finding while also demonstrating a systematic relation between alpha brain rhythm and movement onset. Goodman and Kelso (1983) found further support for synchronization of tremor and movement onset in an experiment investigating both self-paced and time-stressed movements. Analyzing the time from the most recent tremor peak (identified by trained observers) to the onset of movement (defined by movement amplitude exceeding a predetermined threshold), they concluded that people are most likely to begin a movement when they are at the point of maximum velocity in the direction of the intended movement within the tremor cycle.

Critics of Goodman and Kelso's study have pointed out that it was weakened by their use of human observers to determine the time of the most recent tremor peak and by their use of a displacement threshold as a criterion for movement initiation, given that there was no objective starting location from which to measure that displacement (Lakie & Combes, 2000). However, other research has supported a link between tremor and movement onset. Both Parkinsonian tremor and essential tremor have been shown to lead to phase entrainment of voluntary motor reactions (Elble, Higgins & Hughes, 1994; Staude et al, 1995). Interestingly, in the patients studied, this phase entrainment resulted in an onset of voluntary wrist flexion during the extension phase of tremor, which could have impeded movement initiation, rather than during the flexion phase of tremor, which could have aided it. If there is a normal phase relation between tremor generation and muscle activation, then the longer tremor periods found in pathological tremors as compared to physiological tremor might disrupt that relation.

Several researchers have asked whether synchronizing tremor and movement onset leads to a movement time benefit. Lansing, who studied the relations of brain and tremor rhythms to RT, found that the phase of alpha rhythm in which a stimulus was presented had an effect on RT. The phase that was most advantageous varied across participants, suggesting that individual differences in conduction speed must be taken into account when analyzing this sort of data. However, no speed advantage was observed for presentation of the stimulus in any particular phase of the tremor cycle (Lansing, 1957). Lakie and Combes (2000) also failed to find evidence for a speed advantage for synchronization of tremor and movement onset. They presented brief flashes of light to participants as signals to execute a fast wrist flexion. These stimuli were presented at different phases of the wrist tremor cycle. Participants were equally fast regardless of the phase in which the stimulus was presented. There were limitations to both of the aforementioned studies. Lansing prescreened more than 100 people and included as participants only the eight who had the largest cortical alpha rhythms. Therefore his results might not generalize to the population as a whole. However, Lansing's study did provide adequate power,

with 100-200 trials per participant. Lakie and Combes' study, on the other hand, suffered from a lack of statistical power. They also tested eight participants, but each made only 24 moves. Perhaps more importantly, Lakie and Combes also failed to consider that individual differences in conduction speed and reaction time mean that a stimulus appearing in a particular phase in the tremor cycle may be advantageous to one participant and disadvantageous to another. Thus, their finding of no difference is not entirely convincing.

Supposing that, methodological flaws aside, Lansing (1957) and Lakie & Combes (2000) are right, and there is no speed advantage for initiating a movement in a particular phase of a tremor cycle. This does not rule out a functional role for doing so; if movement onset is delayed to wait for the optimal phase in tremor cycle, this would tend to reduce energy expenditure at the expense of reaction time, which might be advantageous in the course of ordinary life. Overall, the evidence suggests that despite the absence of a clear benefit to movement time, movements and tremor are normally synchronized. However, the mechanism behind the synchronization is unknown. Is movement onset delayed, or is the tremor phase reset? Also, note that none of the above mentioned researchers considered the possible existence of fixational limb movements other than tremor in their data. These questions will be addressed later in this thesis.

Bias in Fixational Movement before Voluntary Movement

Another way that fixational limb movement is related to movement onset has recently been discovered. Inspired by recent findings of directional bias in microsaccades before voluntary movement, Cohen and Rosenbaum (2007) examined directional bias in fixational limb movements before voluntary movement. We developed a new approach that involves measuring fixational movements in a limb while the participant anticipates a target-directed movement. In the initial study, participants memorized and then performed simple sequences of pointing movements that included long pauses. Compared to a period of extended stationary pointing, the amplitude of the fixational movement in the axis of forthcoming movement (the main axis) increased, while the direction reversals in the main axis decreased. This was the case when participants pointed with an index finger, and also when the movement occurred only at the wrist, elbow or shoulder. These results show that small limb movements occurring while people are waiting to move give away the axis of intended movement. The source of these effects is unclear, however. If, as has been proposed for other small movements, fixational limb movements reflect aspects of cognition, they will be of great interest to psychologists (some of whom are also movement scientists). If the effects can be shown to reflect a functional contribution of fixational movements to movement initiation, they will be of great interest to movement scientists (some of whom are also psychologists).

Summary of Experiments to be Presented

Following the discovery of directional bias in fixational limb movements, follow-up experiments sought to replicate the effects in different conditions. Additional manipulations were introduced to test several hypotheses regarding the origins and functions of the effects, and also to use the effects to gain insight into other issues in motor preparation. The basic method for testing these hypotheses involved setting up a situation in which participants knew what movement they

would be making next, but they had to wait, maintaining a pointing posture, before executing that movement. The small "fixational" movements occurring while participants waited to move were measured, and the amplitude and frequency of fixational movements in the axis of forthcoming movement were compared to the amplitude and frequency of fixational movements in the orthogonal axis. In Experiments 4-6, RT and MT were also measured.

Experiment 1 tested whether fixational limb movements were affected by the direction of forthcoming movement. Participants watched patterns of movement and stillness and then emulated those patterns by pointing at targets. During the last 500 ms of one-second still periods, fixational movement in the axis of the planned target had greater amplitude and smaller frequency than fixational movement in the axis orthogonal to the planned target, supporting the hypothesis. After this experiment was published (Cohen & Rosenbaum, 2007), the methods for defining movement onset and quantifying amplitude were refined. Only the results of the new analysis (which do not differ substantively from the published results) will be presented. Experiment 1 included four limb segments, while the reanalysis and all subsequent experiments included only movements made at the shoulder joint. Therefore, only shoulder data will be presented here.

Experiment 2 tested whether the effects depended on participants having previously seen the movement, on participants having to self-generate the appropriate waiting interval, or on the specific visual gain used before. Participants performed patterns of movements with pauses as before, but they learned the patterns by hearing descriptions of them rather than by observing them. A laser pointer was used instead of a computer monitor for providing feedback to the participants about their movements, and a metronome assisted participants in maintaining correct timing. The effects were robust to all of these manipulations.

Experiment 3 tested three hypotheses. First, the pause in the center was extended from one second to four seconds. If the effects depended on leftover activation from the previous movement, this manipulation should have eliminated the effects. Second, participants in this experiment were required to perform each pattern twice: once with eyes open and once with eyes closed. If the effects were dependent on vision, there should be effects in the eyes-open condition but not in the eyes-closed condition. Third, the data were analyzed with and without the last submovement during the waiting time. If the effects depended on a single countermove before movement onset in the direction of the target, then there should be effects when the data were analyzed as before, but not when the end of the waiting time was redefined. Extending the pause duration did not eliminate the effects. When the data were analyzed as before, closing the eyes did not eliminate the effects. However, when the last submovement before movement onset was removed from the period under consideration, the frequency effects were eliminated. The amplitude effects remained in the eyes-open condition but were reversed in the eyes-closed condition. Therefore, there appear to be at least two components to the effects. One resembles what is referred to in sports science as the countermove. The other component or components of the effects depend on the availability of vision.

Experiment 4 tested the hypothesis that the effects would be sensitive to cue validity. In this experiment, participants pointed as rapidly as possible to a target indicated by an auditory go cue. Prior to the go cue, they heard a precue which was valid, invalid or neutral with respect to the go cue. This experiment also established a less fatiguing relation to gravity. Participants lay

on a mattress on the floor and pointed at targets on the ceiling. The basic effects were replicated, and the effects were sensitive to cue validity.

Experiment 5 tested the hypothesis that discrete and reciprocal movements are prepared differently. The cued movement task was modified to require discrete (out and wait) moves rather than reciprocal (out and back) moves. Results suggested that reciprocal moves require more planning than discrete moves.

Experiment 6 tested the hypothesis that participants pay attention to the visual information about where they are in the center circle and use it to help them stay in one place, while at the same time being "pulled" in the direction of the forthcoming movement. To test this hypothesis, the size of the center circle was reduced. Results suggested that the amplitude effect was reduced when the staging area size was reduced, consistent with the hypothesis.

Two additional analyses were performed on the data from Experiments 4-6, to test whether the fixational movement effects were functional for movement preparation. The first analysis consisted of tests of correlation between performance measures (RT and MT) and fixational movement effects, both within and across participants. Results indicated that the amplitude effect correlated with movement time across participants, but only when the countermove was included in the fixational movement.

The second additional analysis tested the hypothesis that fixational movement was altered so as to allow movement onset to be synchronized with ongoing oscillation. To test this hypothesis, limb position in the time between the precue and the go cue was averaged across large numbers of trials of each type to create an event-related signal. If phase resetting happens before the go cue, then during the interval between the precue and the go cue, event-related signals should align more closely between conditions that have the same precue than between conditions that have different precues. This result was clearly obtained when participants prepared discrete moves, but not when they prepared reciprocal moves.

CHAPTER 2
EXPERIMENTS BASED ON PERFORMANCE OF MEMORIZED MOVEMENTS

Experiment 1

Recent studies indicate that fixational eye movements reveal the direction of attention or forthcoming voluntary eye or limb movement (Engbert & Kleigl, 2003; Horowitz et al, 2007; Laubrock, Engbert, & Kliegl, 2007). Inspired by this finding, we looked for a similarly informative bias in fixational limb movements before voluntary limb movements. We developed a new approach that involves measuring very small movements in a limb while the participant maintains a posture and anticipates a target-directed movement (Cohen & Rosenbaum, 2007).

In this initial study, participants memorized and then performed simple sequences of pointing movements that included long (1 s) pauses. The pauses were set at 1 s because of evidence showing that readiness is fairly short-duration state, and the preparatory phase preceding voluntary movement normally lasts between .5 and 1.5 s (Deecke, Scheid, & Kornhuber, 1969; Gottsdanker, 1975). We also wanted to minimize fatigue, which is known to increase limb tremor. Moreover, there was concern that if participants were asked to pause for longer than about 1 s, they would begin to mentally subdivide the waiting time, which could leak into the motor system and confound the results (Grondin, Meilleur-Wells, & Lachance, 1999).

Participants were told that the objective of the study was to determine how well they could remember and imitate the timing and sequence of the pattern they had just seen. The task was performed from memory rather than on cue because electrophysiological evidence has shown that self-generated movements activate brain areas associated with motor preparation more strongly than do stimulus-based movements (Waszak, et al, 2005).

If fixational limb movements reflect the intended forthcoming movement, biases should be seen in the amplitudes and frequencies of fixational movements along the axes of voluntary movement.

Method

Participants

The participants were 18 undergraduate students (15 female, 3 male) drawn from the Psychology Department testing pool at Penn State University. They reported no neurological abnormalities. One participant was left-handed and 17 were right-handed. Informed consent was obtained, and the rights and well-being of all participants were protected.

Procedure

The setup for Experiments 1 and 2 is shown in Figure 1. The display marked 'A' was used for Experiment 1. Each participant sat at a table, facing a video monitor 250 cm away. Above the monitor, a bank of three OPTOTRAK cameras (Northern Digital, Waterloo, Ontario, Canada) pointed at the participant. The OPTOTRAK collected three dimensional position data at a

sampling rate of 500 Hz. In the center of the video monitor the participants saw a circle (the central target), 10 cm in diameter, around which were four 10 cm circles at 0, 90, 180, and 270 degrees. The middles of these circles were 15 cm from the middle of the central circle. Thus, the distance from the middle of the center circle to the middle of any peripheral circle was 15 cm, which corresponded to a visual angle of 3.4 degrees ($\tan^{-1}$ (15/250).
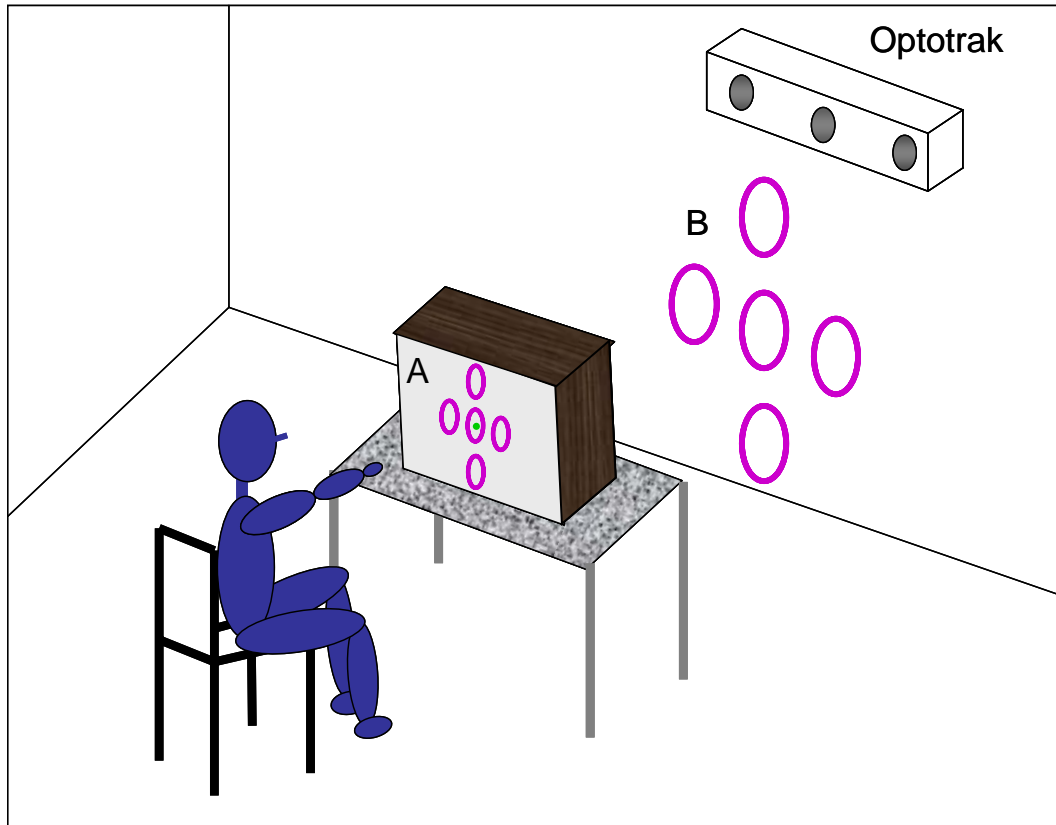
Figure 1. Setup for Experiments 1 and 2. In Experiment 1, participants pointed at targets on a TV monitor and saw a virtual representation of their location (green dot) on the same monitor. In Experiment 2 they pointed at targets on the wall, aided by a laser pointer.

On the monitor, participants also saw a 1.5 cm green dot. In the observation phase of the experimental task, the dot's motion was preprogrammed, but during the baseline task and the reproduction phase of the experimental task the dot's position corresponded to the position of an infrared-emitting diode (IRED) that was attached to the distal end of a light wooden splint worn by the participant. The distance traveled by the fingertip when the participant pointed from the middle of the center circle to the middle of any of the peripheral circles was 23 cm. Thus, for every 1 cm the participant moved, the dot on the screen moved .65 cm.

A brief introduction during which participants verified that they could easily point to all the targets was followed by a short rest. Participants then performed eight experimental trials, each of which consisted of an observation phase followed by a reproduction phase. In the observation

phase, the dot moved from the middle of the bottom peripheral target (the home target) up to the middle of the center target, where it paused for 1 s, then moved to the middle of one of the four peripheral targets (left, right, up, or down), then immediately returned to the middle of the center target, where it paused for another 1 s before returning to the bottom target. Then the entire just-completed pattern was repeated again to complete the sequence. The dot always moved in a straight line from point to point, with a bell-shaped velocity profile. There were four possible sequences, differing only in the direction of the peripheral target to which the dot moved. Each participant was shown each sequence twice, in random order.

In the reproduction phase, the participant brought the dot corresponding to the fingertip to the bottom target. One s later, the screen flashed, indicating that the participant could begin whenever s/he felt ready to do so. To account for the time needed to slow down upon entering the center target and to speed up when leaving it, the dot had to occupy the center target for at least 1.2 s. If this requirement was not met, an error message appeared at the end of the trial. A different error message appeared if the wrong targets were visited or if the correct targets were visited in the wrong order. Following any of these errors, the participant was asked to repeat the trial. All participants successfully completed all trials.

Each participant used his or her dominant arm for the task. Participants completed four variations of both the baseline and pointing sequence tasks. Each variation was the same, except for the joint at which the motion occurred: the metacarpophalangeal joint (index finger movement only), the wrist (hand movement only), the elbow (forearm movement only), and the shoulder (whole arm movement only). For each variation, the participant's active arm was supported and splinted to limit movement to the joint of interest. The gain (i.e., the ratio of depicted cursor movement to actual limb movement) was set so the size of the required movement corresponded to a comfortable range. Three-dimensional position data were collected for the entire replication phase of each trial. Only the two primary movement axes (vertical and horizontal) were considered for analysis.

Data Analysis

Data were filtered with a first order Savitsky-Golay filter with a frame size of 21. This filter was chosen because it did a good job of reducing high frequency (above 20 Hz) components of the signal which could be due to measurement noise, without introducing artifacts at the beginning and end of the data. The adequacy of the filter and parameters were confirmed with visual inspection of raw, filtered, and differentiated data.

A critical step in measuring fixational movements is to define the period of fixation. The end of the fixation period (and thus the start of voluntary movement) was defined as the moment in time when the last reversal of direction in the axis of forthcoming movement before attaining a velocity of 2 m/s. The beginning of the fixation period was defined in an analogous way: as the first moment in time when the direction of movement in the axis of the previous movement (which was always the vertical axis) reversed. Trials in which the period of fixation was less than 500 ms were excluded from analysis. Trials in which the period of fixation was longer than 500 ms were trimmed so that only the last 500 ms were included. When this method was compared to a method relying purely on a velocity threshold, it did a better job of excluding portions of the move toward the target from the defined waiting period.

Typically, Fourier analysis is used to estimate the amplitude and frequency of a signal. This is a statistical method which relies on a minimum of about ten cycles. The period of the movement here was such that there were only a few cycles per stillness period. Furthermore, the cyclicity of the data was questionable. We assumed that the fixational limb movements could include tremor, drift, and jerks. Therefore, Fourier analysis was not an ideal method for approximating the frequencies and amplitudes of oscillation. Instead, four measures were extracted from the identified stillness periods: (1) the standard deviation of the position of the IRED along the horizontal axis, detrended for the overall change in horizontal position; (2) the standard deviation of the position of the IRED along the vertical axis, detrended for the overall change in vertical position; (3) the number of direction reversals along the horizontal axis; and (4) the number of direction reversals along the vertical axis. The stillness period had a fixed duration, so measures (1) and (2) were proxies for amplitude of the fixational movement, and measures (3) and (4) were proxies for frequency.

Each participant's mean amplitude and frequency were computed for each condition. Trials in which there was less than 500 ms of still time were excluded from analysis. If a participant did not have at least one good trial in each direction, his or her data were removed from the analysis. Five participants' data were removed from the analysis because they had too few good trials, and one participant's data were removed because the frequency of fixational movement was greater than three standard deviations above the group mean. The means for the remaining 12 participants were then subjected to ANOVAs.

The data analysis method described above is slightly different from that reported in the published paper, growing out of my ongoing increase in understanding and skill with this kind of data. The new method leads to results that are cleaner and subtly different, but the important results and conclusions are the same.

Results

The effects were similar across the four limb segments tested. However, only the results from the shoulder joint will be shown, because only that joint was used in subsequent experiments. Follow-up experiments were limited to the shoulder because it is well suited for both vertical and horizontal movements (as compared with the elbow, for instance), and because it showed the strongest effects in the initial study.

Amplitude

 The amplitude results are shown in the left panel of Figure 2. There was a significant main effect of axis of oscillation, such that amplitude was greater in the vertical axis than in the horizontal axis: $F(1,12) = 20.l$, $p = .001$. More importantly, there was a significant interaction such that amplitude was greater in the axis of forthcoming voluntary movement than in the orthogonal axis: $F(1,12) = 19.0$, $p = .001$. The difference was larger in the vertical axis ($t = 3.9$, $p = .003$) than in the horizontal axis ($t = 2.0$, $p = .069$).

Frequency

 The frequency results are shown in the right panel of Figure 2. There were no main effects of axis of oscillation or axis of forthcoming movement. However, there was a significant interaction

such that direction reversals were more numerous in the axis orthogonal to the forthcoming voluntary movement than in the main axis: F(1,12) = 10.4, p = .007.
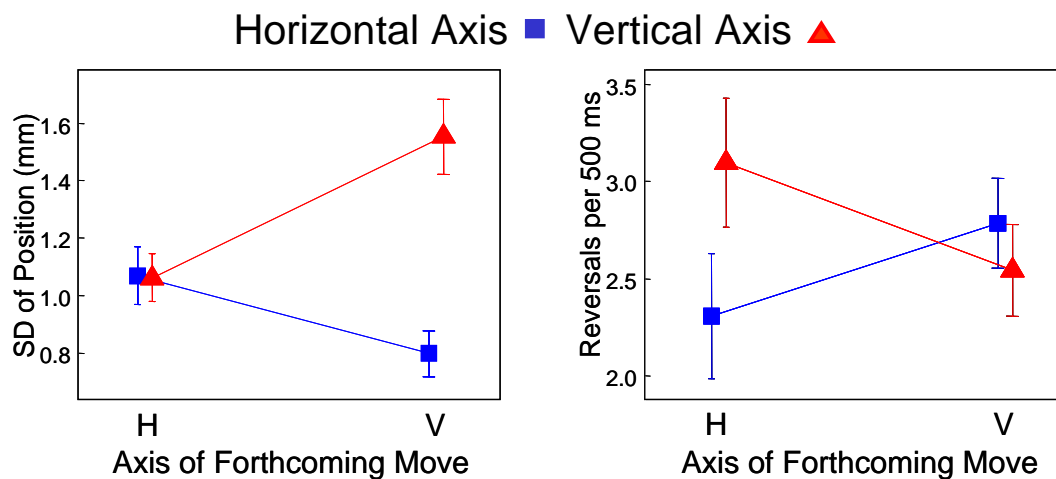
Figure 2. Results from Experiment 1. Left panel: Across participant mean (±1 SE) of standard deviation of position along the horizontal and vertical axes before target-directed movements along the horizontal (H) and vertical (V) axes. Right panel: Across participant mean (±1 SE) number of reversals per 500 ms while holding still in the horizontal and vertical axes, before target-directed movements along the horizontal (H) and vertical (V) axes.

Discussion

Recent studies indicate that fixational eye movements reveal aspects of preparation for a forthcoming voluntary eye or limb movement (Engbert & Kliegl, 2003; Hafed & Clark, 2002; Laubrock, Engbert & Kliegl, 2007). Inspired by these findings, we looked for a similarly informative trend in fixational limb movements before voluntary limb movements. The approach developed here involved measuring very small movements in a limb while participants maintained a posture and anticipated a target-directed movement.

In the experiment discussed here, Experiment 1, participants first watched a dot make a simple pattern of movements and pauses on a screen, and then imitated that series of movements and pauses with their fingertip, while watching a display of their movement on a computer monitor. When participants paused before moving to a target, the amplitude of the fixational limb movements in the axis of forthcoming movement (the main axis) was larger than the amplitude of fixational movements in the axis orthogonal to the main axis. During that same time, the frequency of fixational movements in the main axis was lower than the frequency of fixational movements in the orthogonal axis. These results show that small limb movements occurring while people prepare for a voluntary movement give away the axis of intended movement. Thus, fixational limb movements appear to provide information similar to that provided by fixational eye movements.

The overall amplitude of fixational movements was larger in the vertical axis than in the horizontal axis, as was the difference as a function of forthcoming movement axis. This may have to do with the greater total number of movements performed in the vertical axis than in the

horizontal axis, or with the effect of gravity. Either of these factors would be likely to increase the overall level of activation in the muscles responsible for vertical moves, compared with the muscles responsible for horizontal moves. Alternatively, the difference may reflect some inherent dissimilarity between preparing for movements in different axes with respect to the body or the eyes. The existence of such an asymmetry for fixational limb movements is plausible in light of the fact that fixational eye movements occur disproportionately in the horizontal axis (Ciuffreda & Tannen, 1995). These contrasting possibilities will be investigated in Experiment 4.

These newly discovered fixational limb movement bias effects may comprise a new index of attention and/or a new source of evidence for the cascading of mental activity all the way to the periphery of the system. However, the effects may depend on specific features of the experiment conducted here. For instance, there may be something special about making a series of movements based on having a visual memory of those movements, or about having to monitor the timing of the movements, or about the specific visual gain provided by the setup. The next experiment will vary these factors to test the robustness of the effects.

Experiment 2

In Experiment 1, biases in fixational limb movements occurring while participants waited to move revealed the axis of forthcoming target-directed movements. Experiment 2 was designed to test the robustness of those effects, to ascertain whether they were dependent on specific features of Experiment 1, or more generally reflective of intention or preparatory processes. In this experiment the mode of instruction was changed from observation to description, the visual gain was altered, and participants were given assistance with time monitoring.

The first difference between Experiments 1 and 2 was the mode of instruction. In Experiment 1, participants watched the cursor demonstrate the movement sequence to be produced and then tried to imitate it themselves. In Experiment 2, each movement sequence was verbally described to the participant. A generally accepted idea in cognitive psychology is that visual and auditory working memory are distinct (Baddeley & Hitch, 1974). If the effects obtained in Experiment 1 depended specifically on visual memory of the cursor movement, one would not expect to see similar results with the new method. An advantage of this change in method is that the sequences of movements and pauses could be described much more quickly and efficiently than they can be demonstrated.

Another important difference between the methods in Experiment 1 and Experiment 2 was the removal of self-timing. Time estimation is an effortful process that consumes cognitive resources (see Brown, 1998, for a review). In Experiment 1, participants varied widely in their ability to match their pause lengths to those they observed. For some participants, this was a source of frustration and lost data. Therefore, Experiment 2 removed the requirement that participants estimate the duration of their pauses. If the effects of Experiment 1 depended on self-pacing, they should not be replicated in Experiment 2.

A third difference between Experiment 1 and Experiment 2 was the substitution of computer-generated visual feedback with real-world feedback, in the form of a laser pointer attached to the

end of the splint. This change was made primarily for pragmatic reasons, with the expectation that future experiments might involve placing participants in configurations (such as lying on the floor) in which looking at a computer monitor was inconvenient. However, there was also a possibility that the increase in visual gain created by this alteration would influence the effects.

Method

Participants

Twenty-two Penn State undergraduates (17 female, 5 male) who were enrolled in an introductory psychology course were recruited for the study. All were naïve to the study's purpose, and none had participated in the previous experiment. All participants gave informed consent. Participants used their dominant hands for the experiment; 20 were right-handed, and 2 were left-handed.

Procedure

The setup for Experiments 1 and 2 is shown in Figure 1. The display marked 'B' was used for Experiment 2. Rather than pointing at targets displayed on a computer monitor, participants pointed at targets glued to the wall. As before, the display consisted of a central target circle surrounded by four peripheral target circles at equal distances from the center, to the right (R), left (L), up, (U) and down (D). The diameter of each of the target circles was 50 cm. The distance from the middle of the center circle to the middle of each of the peripheral circles was 90 cm.

Participants received online feedback by means of a laser pointer that was strapped to a light wooden splint, which was in turn strapped to the participant's arm. The distance from the participant's shoulder joint to the wall was 350 cm. For every 1 cm the fingertip moved, the dot projected on the wall by the laser pointer moved 5 cm. The distances moved by the finger when traveling from the center to a peripheral target were approximately 18 cm, which was 20% shorter than the corresponding movements in Experiment 1. The difference came from the need to fit the display on the wall space available.

The distance between the middles of the center and peripheral targets corresponded to 14.4 degrees of visual angle. Thus, for every 1 cm the fingertip moved, the eye moved .824 degrees. The visual gain (the ratio of the change in visual angle to the distance moved by the fingertip) was 5.4 times larger in this experiment than in Experiment 1. This was because the movements represented on the TV monitor in Experiment 1 were smaller than the actual movements, while the movements projected by the laser pointer in Experiment 2 were considerably larger than the actual movements.

Four simple movement sequences were tested in Experiment 2. They were all variations on a common template, so they were easy for participants to remember. These sequences were verbally described by the experimenter before each trial. All trials began at the center target. The basic pattern was: "pause, out, back, home, back," where "out" refers to a different peripheral target every time, "back" refers to a return to the center target, and "home" refers to a movement to the bottom target. This was repeated four times per trial, with every peripheral target visited once per trial. Participants completed four trials. Before each trial, participants were told the order in which they were to visit the four peripheral targets. The orders were R, U, L, D; U, L, D,

R; L, D, R, U; and D, R, U, L. These orders were sequenced in a balanced fashion across participants.

As before, the period of interest was the last 500 ms of the pause preceding a target directed movement. In order to control for immediate history, all pauses followed movements from the bottom peripheral target.

In order to remove the time estimation factor from the experiment, participants' movements were paced with a metronome (set to beep at 300 Hz for a duration of 200 ms at onset intervals of 1000 ms). In time with the metronome, the experimenter said, "Pause…Out, back, down, up, pause; out, back, down, up, pause;" and so forth. Each time the experimenter said, "Out," the participant moved to whichever peripheral target was next, guided by his or her memory of the instructions.

Error monitoring was performed online by the experimenter. If the participant moved to the wrong circle, the trial was redone. If the experimenter failed to catch an error of this sort, the data were discarded at the analysis stage. The use of counting generally prevented early starts.

Data Analysis

Data were filtered with a Savitzky-Golay filter and analyzed according to the method used in Experiment 1. Stillness periods were defined as the last 500 ms before the last reversal of direction in the axis of forthcoming movement. To approximate frequency, the Matlab program counted direction reversals in vertical and horizontal axes. To approximate amplitude, the program calculated the standard deviation of position in each axis.

Data from 7 participants were removed before computing ANOVAs: one because the marker went out of sight at critical times, three because of errors (failing to pause in the center before moving to the target), two because the participants were struggling a lot with the task, and one because the participant's mean amplitude was more than three standard deviations above the group mean.

Results

Amplitude

The amplitude results are shown in the left panel of Figure 3. There was a significant main effect of axis of oscillation, such that amplitude was greater in the vertical axis than in the horizontal axis: $F(1,14) = 45.9$, $p < .001$. There was also a significant main effect of axis of forthcoming target-directed movement, such that amplitude was greater before vertical moves than before horizontal moves: $F(1,14) = 9.1$, $p = .009$. Most importantly, there was a significant interaction such that amplitude was greater in the axis of forthcoming voluntary movement than in the orthogonal axis: $F(1,14) = 8.3$, $p = .012$. The difference was larger in the vertical axis ($t = 3.5$, $p = .004$) than in the horizontal axis ($t = 0.8$, $p = .46$).

Frequency

The frequency results are shown in the right panel of Figure 3. There were no main effects. However, there was a significant interaction such that direction reversals were more numerous in the axis orthogonal to the forthcoming voluntary movement than in the main axis. $F(1,14) = 6.9$, $p = .019$.
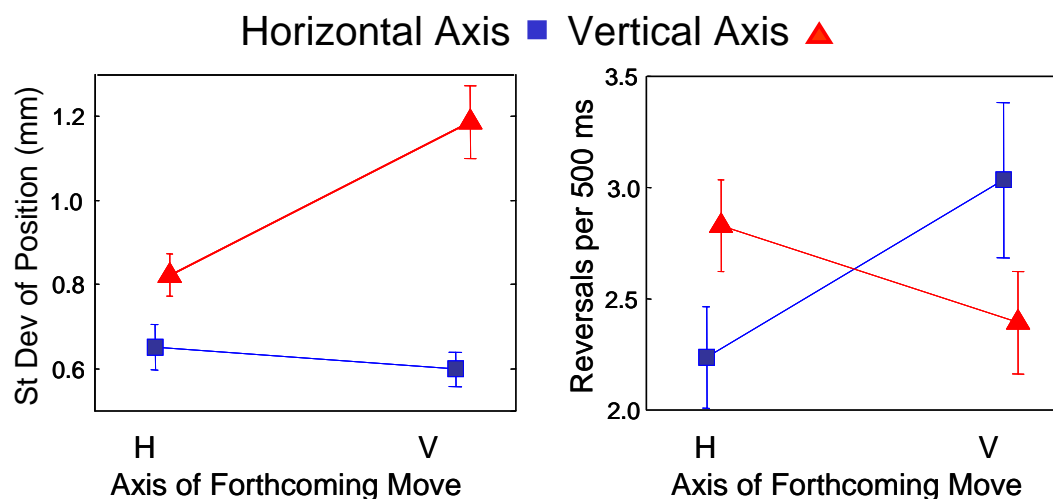
Figure 3. Results from Experiment 2. Left panel: Across participant mean (±1 SE) of standard deviation of position (mm) along the horizontal and vertical axes before target-directed movements along the horizontal (H) and vertical (V) axes. Right panel: Mean number (±1 SE) of direction reversals in each axis, while holding still in the horizontal and vertical axes, before target-directed movements along the horizontal (H) and vertical (V) axes.

Discussion

Experiment 2 sought to determine whether the effects obtained in Experiment 1 were due to three specific features of the method used in that experiment: observational mode of instruction, self-timing, and visual gain of feedback. Participants in Experiment 1 watched the cursor demonstrate the movement sequence to be produced before producing it themselves, whereas participants in Experiment 2 had each movement sequence verbally described to them. Participants in Experiment 1 were required to monitor their own timing, whereas participants in Experiment 2 were provided with a metronome beat to follow. Participants in Experiment 1 saw the results of their movement via a computer monitor, whereas participants in Experiment 2 saw the projection of a laser pointer attached to the end of the splint on their arm.

The results of Experiment 2 echoed those of Experiment 1. When participants pointed at a central target and paused before moving to a previously memorized peripheral target, amplitudes of fixational movements were larger in the axis of forthcoming target-directed movement (the main axis) than in the orthogonal axis, while frequencies of fixational movements were larger in the axis orthogonal to the forthcoming target-directed move than in the main axis. These results demonstrated that the effects were robust to differences in scaling, and to the transfer from a virtual to a real context (i.e., pointing at paper circles with a laser pointer rather than moving a cursor on a video monitor). The effects were not dependent on the participants having previously

seen the required movement as they did in Experiment 1. Therefore, the effects did not depend on visual memory (or mirror neuron activity) but were more specifically associated with intention or motor preparation per se. Furthermore, the effects did not depend on self-timing, as participants in Experiment 2 had a metronome to help them time the movements and pauses.

In all, the results obtained with the new method replicated the results obtained with the old method and indicated that the tendency of fixational limb movements to reveal the axis of forthcoming target-directed movement is robust. This outcome is consistent with the hypothesis that changes in these tiny movements reflect intention to move and may contribute to movement preparation. Because the new method was more straightforward to implement than the previous method, it was used in the subsequent experiment.

Experiment 3

Experiments 1 and 2 established that holding in mind a plan for a forthcoming movement while pointing caused both frequency and amplitude of fixational movements to be different in the axis of forthcoming movement than in the orthogonal axis, and that the effects did not depend on self pacing or perceptual memory. Experiment 3 tested three more predictions regarding the origins of the effects.

In Experiments 1 and 2, participants held still for only 1 s between arriving at the center target from the bottom target and beginning the movement to the next peripheral target. This may not have been long enough for the muscle activity from the "home and back" movement to completely die out. If the effects were driven by muscle activation remaining from the preceding movement, they should be extinguished – or at least severely reduced – with a longer pause. Experiment 3 tested this *Incomplete Damping* prediction. All patterns performed in Experiment 3 included 4-s pauses before main movements.

Another important feature of Experiments 1 and 2 was that participants moved with full vision of their arms and the targets at which they were pointing. Previous studies have indicated that vision plays an important role in the conditioning of fixational limb movements. For example, Chevreul (1833) showed that the kinesthetic illusion of pendulum motion was greatly reduced when the person holding the pendulum closed his or her eyes. Rooks et al (1993) showed that enhanced visual feedback allowed experienced surgeons to reduce their fixational movements, and Morrison and Keogh (2001) showed that enhanced visual feedback caused fixational movements of participants pointing at targets to increase. Therefore, vision could be important for the effects reported here. If the effects obtained in Experiments 1 and 2 were entirely dependent on vision, one would expect them to be eliminated if the task were performed with the eyes closed. Experiment 3 tested this *Vision Dependency* prediction in a within-subjects design, in which all participants moved both with and without vision.

A third prediction regarding the cause of changes in fixational limb movements posits that the effects reflect a single big move in the direction opposite the intended target right before the movement, made to gather elastic energy. This phenomenon, which is commonly seen in endeavors such as jumping and throwing, is known as the countermove (Asmussen, Bonde-

Petersen, & Jorgensen, 1976). The idea that it accounts for the effects seen here will be referred to as the *Countermove Hypothesis*. To test this hypothesis, the data from Experiment 3 were reanalyzed without the last submove. If the effects depend on the countermove, they should be abolished by the removal of the last submove from the data.

These three hypotheses have different implications for the interpretation of the effects. If incomplete damping entirely explains the effects, they may be of limited interest as a tool for studying preparation. If the effects are dependent on vision, experiments investigating the nature of that dependency will be called for, and the effects should be considered in a perception-action framework. If the effects are dependent on the countermove, further investigations of their functionality will be in order.

Method

The basic procedure was the same to that used in Experiment 2. Participants pointed at targets fixed to the wall. A splint was attached to the arm to limit movement to the shoulder joint, and a laser pointer was attached to the end of the splint so participants could monitor their own performance. There were three changes to the procedure. First, the pause between the "home and back" cycle and the "target and back" cycle was extended from 1 s to 4 s. Participants learned a basic movement pattern and were given specific parameters to remember and implement before each trial. Participants heard, "One, two, three, four, out, back, down, up," four times for every trial. During the "four" count, they waited, pointing at the center circle. During the "out" stimulus they moved to the next peripheral target in the remembered sequence, during the "back" cue they moved back to the center circle. During the "down, up" stimuli, participants moved to the bottom (home) circle and returned again to the center circle.

The second change in procedure was the addition of a condition in which participants performed the task with their eyes closed. Each participant performed every trial twice: first with eyes open and then, after a one-minute rest, with eyes closed. In order to maximize possible differences between vision and no vision conditions, one other change was made. The 50-cm diameter circles were replaced with circles that were 11 cm in diameter, while the distance between the centers of the targets was kept the same as before. The reason for the switch to smaller circles was that I thought smaller targets would require more precise aiming and thus would more likely to elicit looking, which would be more likely to provoke a difference between eyes-open and eyes-closed performance.

Twenty-seven undergraduate students (18 female, 9 male) from Introductory Psychology classes at Penn State participated. None had been in any previous experiment in this line of studies, and all gave informed consent. Participants used their dominant arms for the experiment. Five were left-handed, and 22 were right-handed.

Data analysis was performed as before. In addition, the data were reanalyzed with a different definition of the fixation period. Rather than using the last reversal of direction in the axis of forthcoming movement to define the end of the still time, the second-to-last reversal of direction in that axis was used. Everything else about the analysis was the same. Effects were looked for in amplitudes and frequencies of fixational movements in each axis as a function of the axis of forthcoming movement. Data from five participants were excluded from analysis: two for errors

that were not detected until data analysis (moving to the targets in the wrong order), two for the marker going out of sight at critical moments, and one for mean amplitude more than 3 standard deviations from the group mean.

This experiment tested three different hypotheses. If the Incomplete Damping hypothesis is correct, there should be no effects in either condition. If the Vision Dependency hypothesis is correct, there should be effects in the eyes-open condition but not in the eyes-closed condition. If the Countermove hypothesis is correct, there should be effects when the data were analyzed as before, but not when the end of the waiting time is redefined.

Results

Countermove Included

Figure 4 displays the results of the analysis with the end of the fixation period defined according to the last reversal of direction in the axis of forthcoming move. The results for the eyes-open condition can be seen in the upper panels. They are essentially the same as those obtained in Experiment 2. Amplitude (shown on the left) was greater in the vertical axis than in the horizontal axis: $F(1,17) = 32.0$, $p < .001$. Amplitude was greater before vertical movement than before horizontal movement: $F(1,17) = 5.3$, $p = .035$. Of more interest, amplitude was greater in the axis of forthcoming movement than in the orthogonal axis: $F(1,17) = 16.9$, $p = .001$. The effect was strong both in the horizontal axis ($t = 3.1$, $p = .006$) and in the vertical axis ($t = 3.8$, $p = .002$).
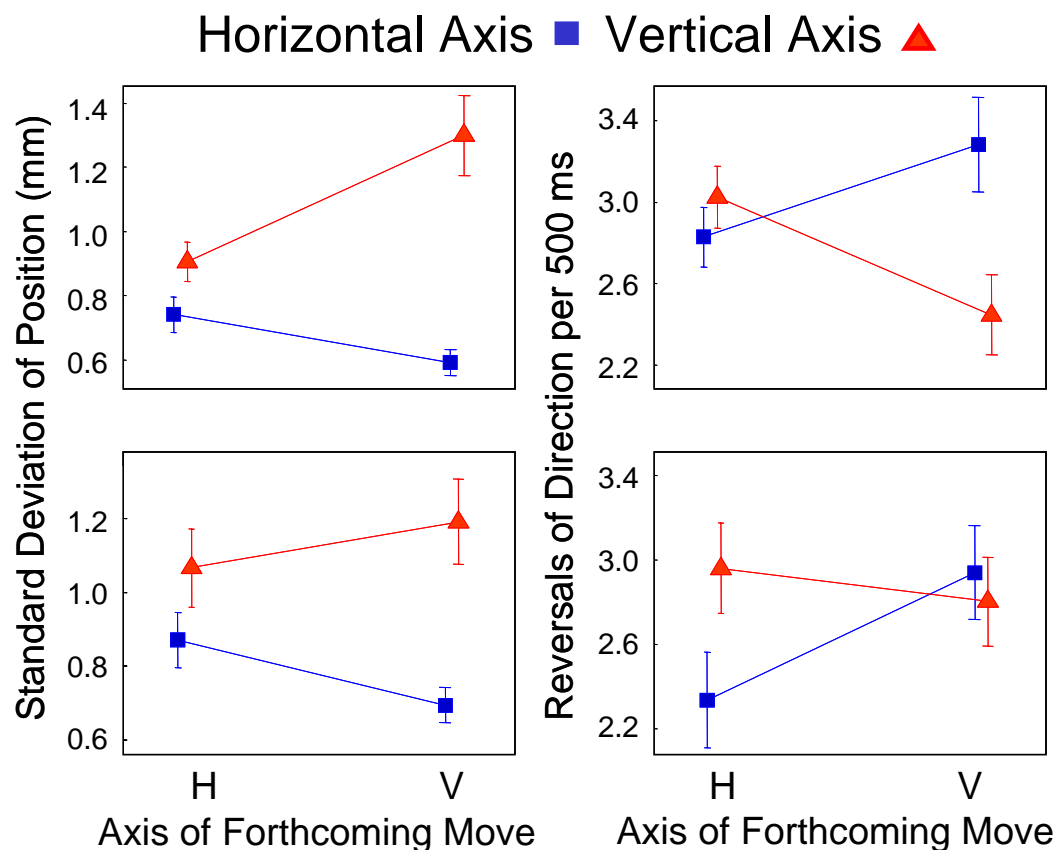
Figure 4. Comparison of results with eyes open (top panels) and eyes closed (bottom panels). Left panels. Across participant mean (±1 SE) of standard deviation of position (mm) along the horizontal and vertical axes before target-directed movements along the horizontal (H) and vertical (V) axes. Right panels. Mean number (±1 SE) of reversals while holding still in the horizontal and vertical axes before target-directed movements along the horizontal (H) and vertical (V) axes.

Frequency with eyes open is shown in the upper right panel of Figure 4. There were no main effects for axis of forthcoming move or axis of fixational movement. However, frequency was greater in the axis orthogonal to forthcoming movement than in the main axis: $F(1,17) = 8.9$, $p = .008$.

The results for the eyes-closed condition can be seen in the lower panels of Figure 4. The pattern looks the same as in the upper panels, and there were no significant three-way interactions between eyes open or closed, axis of forthcoming move, and axis of fixational limb movement, either in amplitude or in frequency. This suggests that closing the eyes did not eliminate the effects. However, 2-way interactions for both the amplitude and frequency effects dropped below significance ($p = .058$ and $.085$, respectively) with eyes closed.

Countermove Excluded

Figure 5 displays results of the analysis with the end of the fixation period defined according to the second-to-last reversal of direction in the axis of forthcoming move. The upper panels

show results from the eyes-open condition. Amplitude effects without the last submove (shown in the left panel) were still significant: $F(1,17) = 14.2$, $p = .002$. However, the effects were reduced compared to amplitude effects with the last submove: $F(1,17) = 7.8$, $p = .013$. Frequency effects from the open-eyes condition are shown in the upper right panel. Neither main effects nor the interaction was significant.
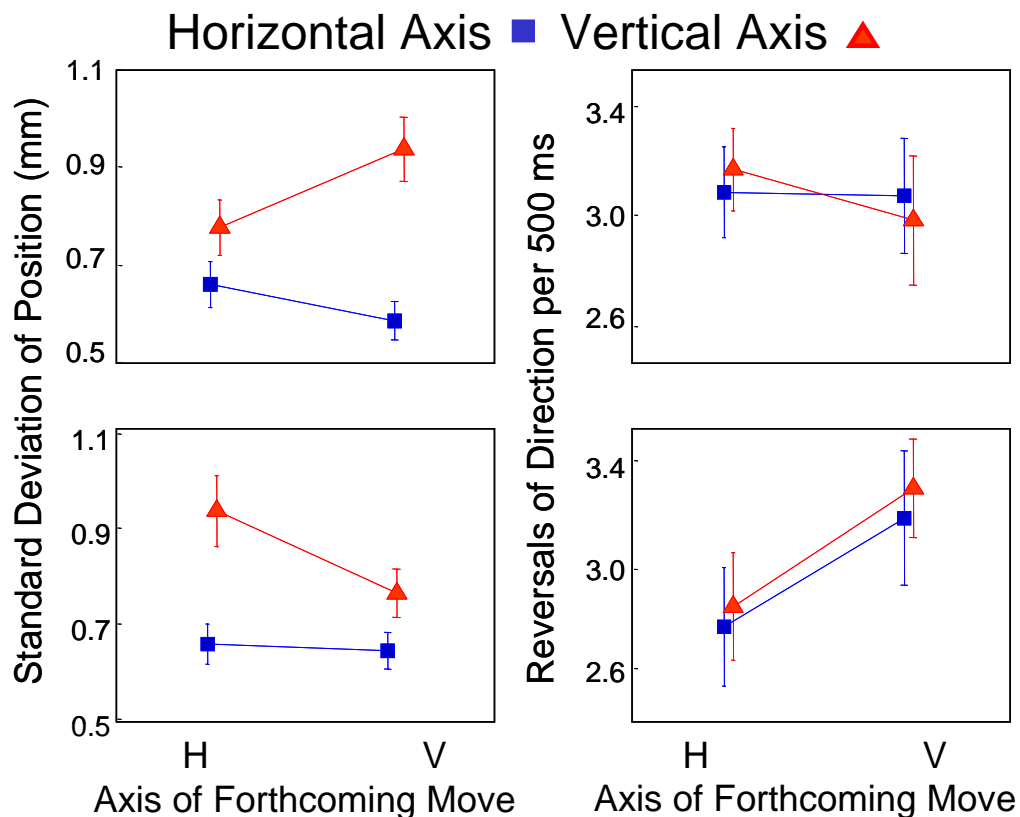
Figure 5. Comparison of results with eyes open (top figures) and eyes closed (bottom figures), with fixation period defined by second-to-last reversal in axis of forthcoming move. Left Figures. Across participant mean (±1 SE) of standard deviation of position (mm) along the horizontal and vertical axes before target-directed movements along the horizontal (H) and vertical (V) axes. Right Figures. Mean number (±1 SE) of reversals while holding still in the horizontal and vertical axes before target-directed movements along the horizontal (H) and vertical (V) axes.

Results from the eyes-closed condition can be seen in the lower panels of Figure 5. As the left panel shows, amplitudes were larger in the vertical axis than the horizontal axis: $F(1,17) = 31.1$, $p < .001$. Furthermore, the vertical amplitudes were larger before horizontal moves than before vertical moves. This pattern is the reverse of that seen in amplitude effects with the last submove. As can be seen in the lower right panel, there were no frequency effects.

Discussion

Experiment 3 tested three new predictions regarding the origins of the effects described in Experiments 1 and 2. These previous experiments established that holding in mind a plan for a forthcoming movement affected fixational movements such that amplitudes were greater in the

axis of forthcoming movement than in the orthogonal axis and frequency was smaller in the axis of forthcoming movement than in the orthogonal axis.

The first question addressed in Experiment 3 was whether the effects were driven by muscle activation remaining from the previous movement. To test this possibility, pauses before movements to peripheral targets were extended from 1 s to 4 s, to give the activation time to fade. Results indicated that extending the pause between arrival from the home target and departure for the next target did not diminish the effects. Therefore, the effects do not depend on selective damping of retained activation from the immediately preceding movement, but are more directly related to the intended movement.

The second question addressed in Experiment 3 was whether vision was critical for the effects. If so, the effects should have been eliminated when the task was performed with eyes closed. To test this possibility, all participants moved both with and without vision. When the data were analyzed as before, there was no difference between the effects in the eyes-open and eyes-closed condition. Therefore, the effects are not entirely reliant on vision.

The third question addressed in Experiment 3 was whether the effects depended on a single countermove – the last submove before movement begins in the direction of the target. When the data were reanalyzed without the last submove in the axis of forthcoming movement, marked differences between the eyes-open and eyes-closed conditions appeared. In the eyes-open condition, amplitude effects were reduced compared to the original analysis, and frequency effects were eliminated. In the eyes closed condition, the direction of the amplitude effect reversed.

Two conclusions may be drawn from these results concerning the countermove. First, the countermove is a relevant factor in the establishment of bias in fixational limb movement prior to voluntary movement. This was particularly true for the frequency effect even with eyes open, and for both effects with the eyes closed. Second, contrary to the preliminary conclusion drawn after the first analysis of the data, it seems that vision is important for the elicitation of fixational limb movement effects, especially for the amplitude effect *prior to the countermovement*.

As a side comment, the literature regarding countermovement refers exclusively to preparation for powerful ballistic movements such as jumping as high as possible and throwing at high speeds. However, this laboratory demonstration of a countermove before a moderately paced movement is consistent with informal observations of everyday movement and slower-paced sports. For instance, a golfer preparing for a gentle putt uses a backswing that can be likened to a countermove.

The finding that vision had an influence on fixational movements is consistent with previous findings on the effects of vision. Recall that vision was implicated in the pendulum illusion (Chevreul, 1833), and enhanced vision has been shown to affect hand steadiness either for the better (Rooks et al, 1993) or for the worse (Keogh, Morrison & Barrett, 2004). The mechanism of the influence is unknown, however. One possibility in the current context is that participants looked back and forth between the home and target circles while waiting to move, and the eye exerted a coupling influence on the arm. Such a mechanism is plausible in view of the well-established fact that there is functional coupling between the eyes and the hand during visually

guided aiming (Abrams, Meyer, & Kornblum, 1990; Gribble, Everling, Ford, & Mattar, 2002; Herman, Herman, & Maulucci, 1981; Reina & Schwartz, 2003; c.f. Henriques et al, 2003; Steinman et al, 2003). Another way that vision could play an important role in fixational movements is that participants may use visual feedback to stay in the center circle before the initiation of the voluntary movement. According to this hypothesis, participants drift in the direction of the planned target-directed move, are alerted by visual feedback that they have drifted, and make a correction. Because this hypothesis claims that participants move in the direction of the target before they intend to initiate movement, it is consistent with the claims of cascading activation models. Experiment 6 will further investigate the influence of vision on fixational movements.

Stepping back and looking over the results of all three of the experiments reported so far, the experiments established that holding in mind a plan for a forthcoming movement affects fixational movements such that amplitudes are greater in the axis of forthcoming movement than in the orthogonal axis and frequency is smaller in the axis of forthcoming movement than in the orthogonal axis. The effects do not depend on self pacing, perceptual memory, or activation remaining from the previous move. However, they are partially dependent on the countermove and partially dependent on vision. All of these findings are consistent with the hypothesis that changes in fixational limb movements reflect readiness to move.

CHAPTER 3
CUING STUDIES

In experiments 1-3, participants planned a whole movement sequence before they began. This method did not allow the experimenters to observe participants during the planning of target-directed moves. The next set of experiments addresses this deficiency by implementing a cuing method. With this method, participants could not plan a target-directed move until they were informed as to which target was next. In addition to facilitating the observation of participants while they planned each move, the cuing method introduced two baseline conditions, allowed the time-locking of data to presentation of a stimulus, and balanced the number of moves in each axis.

Another feature of the new method is a change in the orientation of the participants with respect to gravity. In the new method, the participants lay down and pointed up rather than sat and pointed out. This change was made for two reasons. First, it reduced fatigue, and so allowed for the collection of more data per participant. Second, it addressed the asymmetry in the amplitude effect that was present in all three initial experiments. Especially in Experiments 1 and 2, amplitude effects were stronger in the vertical axis than in the horizontal axis. These features of the data may have been due to participants' coping with gravity.

Three experiments are presented in this chapter: Experiments 4, 5, and 6. Experiment 4 introduced the new method and tested whether the effects were sensitive to expected stimuli. Experiment 5 used the method to ask whether discrete movements and reciprocal movements were prepared differently. Experiment 6 provided enhanced visual feedback to test the possibility that increases in fixational movements in the axis of forthcoming movement were caused by repeatedly drifting toward an intended target and then correcting for that drift. Motivations for the two major changes to the method are described below.

After the three experiments are presented, two additional analyses are described. These analyses tested two hypothesized ways that changes in fixational movements could facilitate preparation for voluntary movement. They are presented separately because the hypotheses they address are separate from the hypotheses tested in each individual experiment.

Cuing

In all the experiments described up to this point, participants pointed at targets recalled from memory. A decision to use this approach rather than to rely on external cues to trigger the movements was originally made because movements to recalled targets were considered to be similar to self-generated movements, which have been shown to activate brain areas associated with motor preparation more strongly than do stimulus-based movements (Waszak et al, 2005). Therefore, it was possible that switching to a cuing method would eliminate the effects. However, if the effects were replicable with a cuing method, this would attest to the robustness of the effects and would have some methodological advantages.

One important advantage of the cuing method is that it gives the experimenters more control over the timing and accuracy of the information that participants receive about the forthcoming

movement. Providing participants with misleading information (invalid precues) allows the experimenters to observe participants' behavior as they change their minds. Future studies could also investigate whether giving participants partial information affects the results.

Another advantage of a cuing method is that, rather than controlling for history by making sure every target-directed move follows a move from the same home target, every direction of movement can occur after every other direction of movement an equal number of times. This allows for cancellation of the influence of recent history without all the extra moves required by the methods used up to now. The cuing method thus allows for collection of twice as much data from each participant in the same amount of time, without requiring more moves in one axis than another. In addition, pilot work suggested that participants stay attentive and engaged for longer with the cuing method than with the memorization methods.

Yet another advantage of the cuing method is that it provides two different baseline conditions: a control condition in which participants know that they will not be asked to move to a target imminently, and a neutral condition in which they know they will be asked to move to a target but don't know which one. The inclusion of these baseline conditions allows conclusions to be drawn about absolute increases or decreases in fixational movements rather than just comparisons between axes. This could potentially allow for the discovery of more complex relations between fixational and voluntary movement, such as an overall decrease combined with a selective increase in one axis.

A final advantage of the cuing method is that the target-directed movements are speeded. Thus, tests can be run to see whether reaction time and movement time, which are commonly accepted measures of readiness, correlate with either of the fixational limb movement effects. Correlations between the effects and other measures of readiness would support the idea that the fixational limb movement effects are a functional part of preparation.

The cuing method used here was similar to standard cuing studies used elsewhere in psychology, neuroscience, and kinesiology (e.g., Posner, Snyder & Davidson, 1980). Subjects pointed to a central target and waited for a go signal, which was preceded by a precue. Upon hearing the go signal, they pointed as quickly as possible to the target indicated, then returned to the center circle. The cues were auditory sound files played by the computer. They consisted of color words that matched the four peripheral targets (green, red, blue and yellow), as well as "stay" for control conditions and "wait" for neutral conditions. In the control trials, participants remained pointing at the center circle. This provided a baseline condition against which the trials involving movement preparation could be compared. In neutral trials, participants were to prepare for a movement but were not given directional information. This allowed assessment of the effect of the directional information in the precue. The time interval between the direction cue and the go signal remained constant. Based on many published cuing studies, I expected that reaction time (RT) would be faster when the two cues matched than when they didn't match, indicating that participants used the first cue to prepare for the arrival of the second one and for subsequent action. I expected RT in the neutral condition to be between the valid and invalid RTs.

New Relation to Gravity

In Experiments 1-3, participants made a total of 4-8 moves to each peripheral target. The number of moves was kept low to reduce fatigue. In order to have enough trials to include adequate numbers of valid, invalid and control trials in every direction, the issue of fatigue needed be addressed. One obvious source of fatigue in the experiments conducted so far was the requirement to hold the arm up against gravity while pointing at the center circle and waiting to move. To reduce this fatigue, participants in the cuing studies were asked to lie on a soft foam mat on the floor and point at targets on the ceiling. Pilot trials suggested that this method is comfortable and relatively non-fatiguing. In this position, the arm is balanced, and very little effort is required to maintain the position. Thus the level of background muscle activation should be lower than when participants pointed at the wall.

In addition to reducing fatigue, changing the relation of the participants to gravity allows investigation of a previously unresolved issue in the data, which was the pronounced asymmetry in the amplitude effect. In Experiments 1-3, both overall amplitude and amplitude effects were stronger in the vertical axis than in the horizontal axis. One possible explanation is that there is something inherent to the physiology or psychology of movement preparation such that movements made in the axis of the body require more preparation than movements in the lateral axis. A more straightforward explanation is an imbalance in the aforementioned fatigue. Maintaining a pointing posture requires the use of muscles to hold the arm up against gravity. These are in large part the same muscles that initiate and terminate voluntary movements in the vertical axis. Therefore, these "vertical mover" muscles were used much more than the muscles that initiated and terminated horizontal moves. The imbalance was further exaggerated by the fact that the home-and-back movements were in the vertical axis, and could lead to greater fatigue in the vertical movers than in the horizontal movers. Fatigue is known to enhance physiological tremor (Deuschl, Raethjen, Lindemann, & Krack, 2001). If the muscles responsible for vertical movements were fatigued but the muscles responsible for horizontal moves were not, greater tremor would be expected in the vertical axis. If the amplitude asymmetry was due to this difference in the engagement of the two sets of muscles, then the results should be more symmetrical when this difference is removed. However, if the amplitude effect was dependent on the high background level of activation necessary to hold the arm up against gravity, this manipulation should eliminate the effects altogether. The supine position, in addition to reducing overall fatigue, promotes a more balanced use of arm muscles. The cuing method, which eliminates the extra home-and-back movements, further promotes balanced use of the muscles.

Experiment 4

Method

Participants

Twenty-five undergraduate students (16 female, 9 male) were drawn from the undergraduate psychology testing pool at Penn State University. All were naïve to the study's purpose, and none had participated in any previous experiment in this line of research. Participants gave

informed consent and filled out handedness assessments. Twenty-two of the participants were right-handed, and 3 were ambidextrous. All used their right arms for the experiment.

Procedure

The setup for Experiments 4-6 is shown in Figure 6. Five targets were displayed on the ceiling, in the same pattern as in previous studies. The circles were made of colored paper. The center circle was black, and the peripheral circles were red, green, yellow and blue. The targets were 36 cm in diameter and their centers were 81 cm apart. The ceiling was 2.75 m high. Participants lay on a foam mattress with the shoulders of their dominant arms centered beneath the center circle of the display. The splint, IRED, and laser pointer were attached as in previous studies.
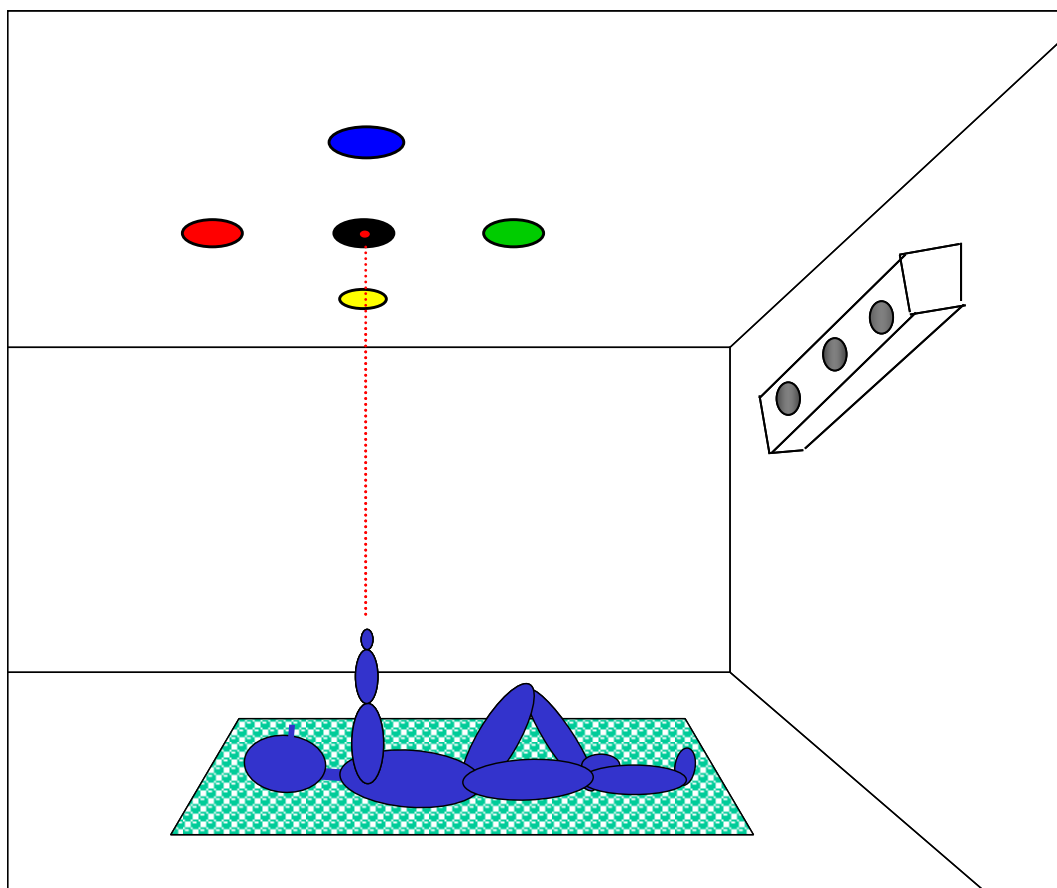
Figure 6. Setup for Experiments 4-5. Participants lay on a foam mat and pointed upward with a laser pointer. (Setup for Exp 6 was identical, but with a smaller center circle.)

Pre-recorded auditory stimuli were delivered to the participants by way of small speakers set by their heads. For every trial, participants heard a pair of two words, with a stimulus onset asynchrony (SOA) of 800 ms. This SOA was selected based on pilot trials indicating it led to the greatest feeling of readiness. Cuing studies often use flashes of light as stimuli. These are processed much more quickly than words, and thus require shorter SOAs to maximize readiness (Posner, Snyder, and Davidson, 1980). Control trials consisted of the word 'stay' repeated twice. Neutral trials consisted of the word 'wait' followed by a color name. Valid trials consisted of a

single color name repeated twice. Invalid trials consisted of two different color names. Of note, the color names in invalid trials could indicate targets that were in opposite directions from each other and thus in the same axis ('opposite' trials), or they could indicate targets that were adjacent to each other and thus in orthogonal axes ('adjacent' trials).

Participants were instructed to remain pointing at the center of the center circle until they heard the second cue, then to move as quickly as possible to the center of the circle named and back to the center to wait for the next pair of words. The next precue arrived 3200 ms after the previous go cue; thus, the total time for a trial was 4 s. Trials were presented in blocks of 20, after which participants rested their arms at their sides. There were 20 blocks, for a total of 400 trials. Of these, 200 were valid, 40 were control, 80 were neutral, 40 were opposite and 40 were adjacent. The order of the directions and trial types was randomized across 5 sets of 4 blocks. The whole experiment took approximately 45 minutes.

Data Reduction

Data were filtered and movement onsets were determined as previously described. Trials were sorted according to cue validity as well as axis of forthcoming movement. The number and amplitude of fixational movements were computed in each axis as before. In addition, reaction times were computed as the time between the onset of the go cue and movement onset, and movement times were computed as the time between movement onset and the subsequent direction reversal at the target.

Errors were defined as trials in which participants moved to the wrong target or initiated movement to the target too soon (less than 100 ms after the go cue) or too late (more than 1000 ms after the go cue). Most of these errors occurred early in practice. Trials with errors were removed from analysis. Trials were also removed from analysis if the marker went out of sight of the camera (due to the subject rotating the arm), if an experimenter error was discovered during analysis (such as running the same set of trials twice in a row), or if the amplitude of the fixational movement was more than three standard deviations from that subject's mean amplitude, for that direction and cue validity. The average participant had 300 good trials after removal of errors and outliers.

In order to compare the strengths of the amplitude and frequency effects across conditions, the effects were expressed as a single number. The amplitude effect for each participant was defined as the mean ratio of the amplitude in the axis of forthcoming movement to the amplitude in the orthogonal axis, across trials. The frequency effect was defined as the ratio of the number of direction reversals in the axis of forthcoming movement to the number of direction reversals in the axis orthogonal to forthcoming movement. Thus, for each effect, a null result would result in a ratio of 1, and anticipatory bias would result in a ratio greater than one.

Results

Figure 7 shows RT for trials with different cue validity for Experiments 4-6. Results from Experiment 4, in which participants made reciprocal (out-and-back) moves, are shown in the left panels. As predicted, RTs were faster (316 ms) for valid trials than for neutral, opposite or adjacent trials (387, 388, and 409 ms respectively). $F(1,39) = 37.5$, $p < .001$. RTs to neutral trials

were slightly faster than to adjacent trials (p = .036). RTs to opposite trials were marginally faster than RTs to adjacent trials (p = .062).
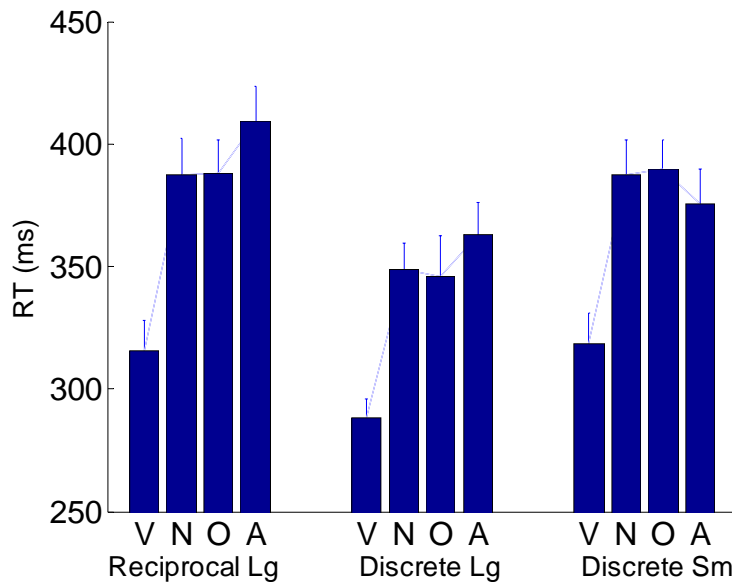
Figure 7. Reaction times for valid (V), neutral (N), opposite (O), and adjacent (A) conditions. Left panels: Experiment 4. Middle panels: Experiment 5. Right panels: Experiment 6.

Figure 8 shows Movement time (MT) for trials with different cue validity. Results from Experiment 4 are shown in the left panels. MT was faster for valid trials (432 ms) than for neutral, opposite or adjacent trials (479, 498, and 480 ms respectively). $F(3,57) = 8.0$, $p < .001$. There were no significant differences among neutral and invalid conditions.
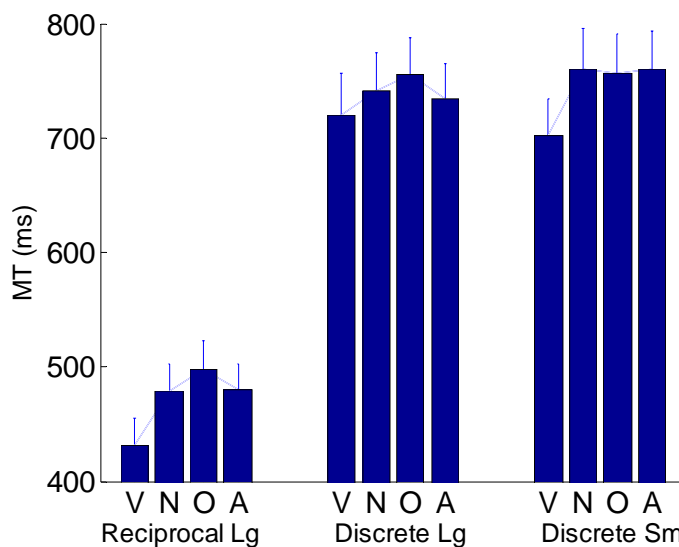
Figure 8. Movement times for valid (V), neutral (N), opposite (O), and adjacent (A) conditions. Left panels: Experiment 4. Middle panels: Experiment 5. Right panels: Experiment 6.

Figure 9 shows the amplitude and frequency of fixational movement in each axis, for the valid trials only, during the last 500 ms before movement onset. As was seen in previous studies, both amplitude and frequency of fixational movement reflected the axis of forthcoming movement. Amplitude (left panel) was greater in the axis of forthcoming target-directed movement than in the orthogonal axis. For a one-sample t-test comparing the ratio of movements in the two axes to 1.0, $t(19) = 7.3$, $p < .001$. Relative to the baseline, amplitude showed both an increase in the axis of forthcoming target-directed movement and a decrease in the orthogonal axis, and the effect was balanced in both axes.

The right panel of Figure 9 shows frequency of fixational movements during the waiting period. Overall, frequency was lower in this experiment than in the previous Experiments. However, the predicted interaction remained robust. Frequency was greater in the axis orthogonal to the forthcoming move than in the main axis. For a one-sample t-test comparing the ratio of movements in the two axes to 1.0, $t(19) = 8.7$, $p < .001$. Relative to the baseline, the decrease in the axis orthogonal to the forthcoming target-directed move was more prominent than the increase in the main axis.
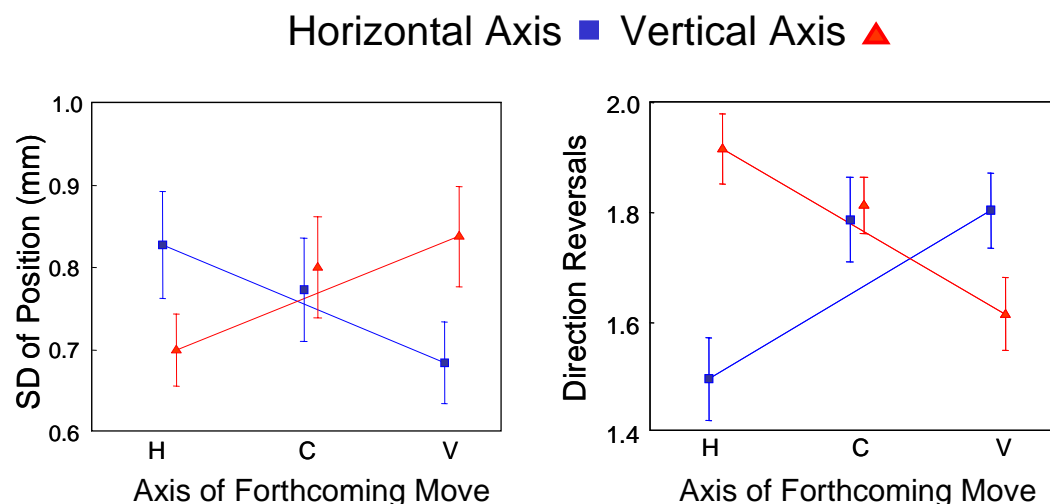
Figure 9. Left Panel. Across participant mean (±1 SE) of standard deviation of position (mm) along the horizontal and vertical axes before target-directed movements along the horizontal (H) and vertical (V) axes. Right Panel. Mean number (±1 SE) of direction reversals in each axis, while holding still in the horizontal and vertical axes, before target-directed movements along the horizontal (H) and vertical (V) axes.

Cue Validity Effects

The left panels of Figure 10 show the influence of cue validity on amplitude effects for Experiment 4. The magnitude of the amplitude effect is expressed as a ratio of amplitude in the axis of forthcoming movement to amplitude in the orthogonal axis, such that a null effect would be expressed as a ratio of 1. Cue validity had an influence on the effects, such that effects were present in valid and opposite trials, absent in neutrals trials, and reversed in adjacent trials. $F(3,57) = 33.9$, $p < .001$. In sum, amplitude increased in the precued axis, whether that axis was also the axis of eventual movement (as in opposite and valid trials) or not (as in the adjacent trials).
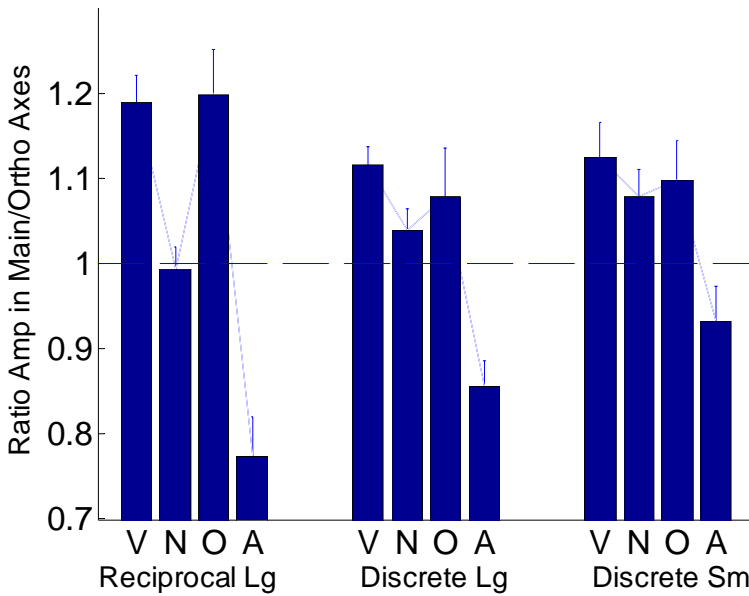
Figure 10. Cue validity influence on amplitude effect for Experiments 4-6. Ratio of amplitude in axis of forthcoming movement to amplitude in orthogonal axis. Left panels: Experiment 4. Middle panels: Experiment 5. Right panels: Experiment 6. Conditions: valid (V), neutral (N), opposite (O), and adjacent (A).
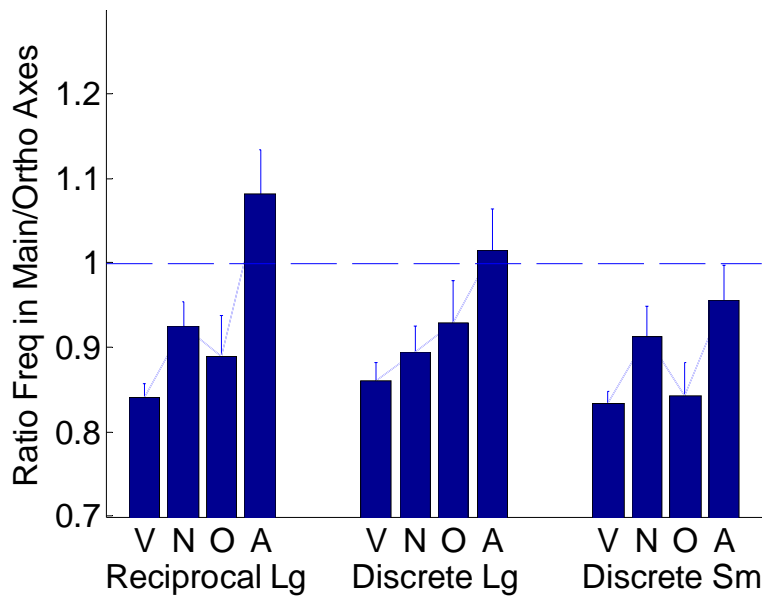
Figure 11. Cue validity influence on frequency effect for Experiments 4-6. Ratio of number of direction reversals in the axis of forthcoming movement to number of direction reversals in the orthogonal axis. Left panels: Experiment 4. Middle Panels: Experiment 5. Right panels: Experiment 6. Conditions: valid (V), neutral (N), opposite (O), and adjacent (A).

Figure 11 shows frequency effects for Experiments 4-6, expressed as a ratio of frequency in the axis of forthcoming movement to frequency in the orthogonal axis, such that a null effect would be expressed as a ratio of 1. Cue validity had an influence, such that effects were smaller in the adjacent trials than in the valid, neutral, or opposite trials. $F(3,57) = 7.3$, $p < .001$. Valid trials had a slightly larger effect than neutral trials ($t = 2.2$, $p = .039$).

Discussion

Experiment 4 investigated fixational movements between target-directed moves in a cuing paradigm. Participants listened and responded to pre-recorded pairs of words in which the first was the precue and the second was the go cue. They were instructed to remain pointing at the center of the middle circle until they heard the go cue, then to move as quickly as possible to the center of the circle named by the go cue and back to the center of the middle circle, where they would wait for the next pair of words. The use of pairs of cues allowed the inclusion of valid, invalid, neutral and control trials. In control trials, both the precue and the go cue consisted of the word 'stay.' In neutral trials the word 'wait' was followed by a color name. Valid trials consisted of a single color name repeated twice. Invalid trials consisted of two different color names, which could either indicate targets that were in opposite directions from each other ('opposite' trials) and thus in the same axis, or targets that were adjacent to each other ('adjacent trials') and thus in orthogonal axes.

To verify that a precue captured participants' attention effectively, experimenters typically look for faster RTs in valid trials and slower RTs in invalid trials. In this experiment, RTs were approximately 60 ms faster for valid trials than for neutral, opposite or adjacent trials, indicating that participants were attending to the precues. There was a small cost for adjacent trials relative to neutral trials, but no cost for opposite trials relative to neutral trials. This was a surprising result. Apparently when participants discovered that they had prepared for the wrong movement, they were able to quickly correct and make up some of the lost time.

The amplitude effect remained strong in this experiment. Relative to the baseline, amplitude showed a balanced increase in the axis of forthcoming target-directed movement and a decrease in the orthogonal axis. Of note, the asymmetry that was seen in the amplitude effect when the task was performed pointing at a wall (Experiments 1-3) was now gone. There was no main effect of axis of fixational movement, and the effect of forthcoming move was significant in both axes. Thus, the previously observed asymmetry in amplitude was most likely due to the need to hold the arm against gravity in the vertical axis during the still time. That the effects remained strong despite the less fatiguing method indicates that fatigue was not the sole source of the effects.

Overall, the frequency in this experiment was lower than in the previous experiments. Most likely this had to do with the relative state of relaxation that participants were in, lying supine and pointing straight up. However, the frequency effect remained strong. Relative to the control trials (no immediate planned movement), frequency in valid trials increased in the axis orthogonal to forthcoming movement and decreased in the main axis. The decrease was more prominent than the increase. Thus, the effect is more reliant on a reduction in number of direction reversals in the axis of forthcoming movement than on an increase in the axis orthogonal to forthcoming movement.

Cue validity had an influence on the amplitude effects. Amplitude increased equivalently in the axis of forthcoming movement relative to the orthogonal axis for all the trials in which the precue and the go cue were in the same axis (valid and opposite trials). Amplitude in each axis was equal before neutral trials. Before trials in which the precue and the go cue were in different axes, the amplitude increased in the axis of the precue, not the axis of the go cue and eventual movement. Thus, the effects reflect the processing of the precue.

Cue validity also influenced frequency effects. The greatest effects were seen for trials with precue and go cue in the same axis, and the smallest effects were seen for trials in which the precue and go cue were in different axes. The bias in frequency was also present in neutral trials, suggesting that the effect reflected preparatory activity that occurred after the go cue had been somewhat processed.

The results of this experiment illuminate several aspects of the changes in fixational movements before voluntary movement. The results reveal that the fixational movement effects do not depend on prior memorization of the directions of voluntary movements, nor do they depend on fatigue. The results also reveal that the effects are susceptible to manipulation of cue validity and thus are reflective of expectation. In addition, the inclusion of baseline conditions reveals that the effects rely on both increasing activity in one axis and decreasing activity in the orthogonal axis. Furthermore, differences between the amplitude effect and the frequency effect suggest that the amplitude effect reflects mainly processing of the precue, while the frequency reflects processing of both the precue and the go cue. Finally, these effects coincided with the replication of the classic finding for a cuing experiment. There was a reaction time advantage for trials with valid cues as compared with trials with invalid cues, as well as a small movement time advantage for trials with valid cues. Thus, this method adds to the arsenal of tools available for investigating preparation. The next experiment makes use of the method in this spirit.

Experiment 5

In all the experiments reported so far, target-directed movements were reciprocal, that is, out-and-back. The fifth experiment investigated the degree to which the effects depended on that feature of the task. The purpose was to determine whether preparation is different before discrete and reciprocal moves, and, in doing so, to perhaps cast some light on the status of a single reciprocal move in the pantheon of discrete and cyclic moves.

Cyclic movements are kinematically, biomechanically, and neurally different from discrete movements. Kinematically, the difference is that discrete movements must achieve zero acceleration at the end points, whereas cyclic movements continue to negatively accelerate (Hogan & Sternad 2007). Biomechanically, cyclic movements allow actors to take advantage of the elasticity of their muscles, thus requiring less force (Guiard, 1993). Neurally, discrete movements activate additional brain areas beyond those used for cyclic movements (Schaal, Sternad, Osu & Kawato, 2004).

Several possible relations between the two types of movement have been proposed. One perspective, put forth by Schöner (1990) holds that all movement is essentially cyclic. Thus, a

reciprocal move is formed by planning and truncating a cyclic movement, and a discrete move is formed by planning and truncating a reciprocal move. (Since the movements in Experiment 4 were reciprocal rather than cyclic, the latter part of Schöner's proposal is of particular interest.) A contrasting perspective holds that a reciprocal move is formed by planning and concatenating two discrete moves: one to the target and one back (van Mourik & Beek, 2004). A third possibility, supported by evidence from several sources, is that discrete and reciprocal moves belong to two different classes, such that neither is built from the other (Hogan & Sternad, 2007; Huys et al, 2008).

Experiment 5 was identical to Experiment 4, with one critical difference: the introduction of discrete target-directed movement. Instead of moving as quickly as possible to the peripheral target and back to the center, participants moved rapidly to the peripheral target and waited 3 s for a signal to return to the center. There is precedent for using RT as a measure of complexity of preparatory processes (Fischman & Lim, 1991). The basic idea is that movements that entail more complex processes will take longer to complete. This experiment used both RT and the previously described anticipatory bias effects to evaluate the complexity of preparatory processes before discrete and reciprocal movements.

If reciprocal moves are concatenations of discrete moves, then reciprocal moves should be slower to initiate than discrete moves, because the planning would involve the stringing together of two discrete moves. Therefore, RTs should be faster in Experiment 5 than they were in Experiment 4. Furthermore, discrete moves should demonstrate reduced anticipatory effects relative to those seen in Experiment 4. If, on the other hand, discrete moves are truncated reciprocal moves, they should be slower to initiate than reciprocal moves, because a plan for a reciprocal move would need to be generated and then edited. Furthermore, discrete moves should show enhanced anticipatory effects relative to Experiment 4.

Method

Participants

Twenty-three new participants (12 female, 11 male) were drawn from the undergraduate psychology testing pool at Penn State University. None reported any neurological abnormalities. All were naïve to the study's purpose, and none had participated in any of the previous experiments in this line of work. All participants gave informed consent and filled out handedness assessments. Eighteen of the participants were right-handed, 3 were right-handed, and 2 were ambidextrous. Participants used their dominant arms for the experiment. Those who reported themselves as ambidextrous were given a choice of which arm to use after the task was described to them. Each chose to use the right arm.

Procedure

The physical setup was identical to that used in Experiment 4, as shown in Figure 6. The basic method was the same, in that participants pointed to the center circle and listened to pairs of cue words, then moved as rapidly as possible to the second color named. However, rather than return immediately back to the home circle, participants were instructed to wait in the center circle for a signal to return home (the word 'home'). They were told that movement to the home circle did

not have to be fast. The SOA between precue and go cue was again 800 ms. The SOA between the go cue and the home signal was 2000 ms. This was followed by a space of 2200 ms before the next precue, for a total trial time of 5 s.

Trials were presented in blocks of 16, after which participants rested their arms at their sides for approximately one minute while the experimenter set up the next trial. There were 16 blocks of trials, for a total of 256 trials. The ratios of trial types were the same as before. Thus, each participant performed a total of 128 valid trials, 64 neutral trials, and 32 each of control, adjacent, and opposite trials. The order of the directions and trial types was randomized across 4 sets of 4 blocks. The whole experiment took approximately 45 minutes.

Data reduction was exactly the same as in Experiment 4. After removal of errors and outliers, each participant had an average of 195 good trials.

Results

The middle panel of Figure 7 shows RT for trials with different cue validity for Experiment 5. As in Experiment 4, RTs were faster for valid trials (288 ms) than for neutral, opposite or adjacent trials (349, 346 and 363 ms respectively). $F(3,60) = 20.8$, $p < .001$. There were no significant differences among neutral and invalid trials. Overall, reaction times were approximately 40 ms faster here than in Experiment 4. $F(1,39) = 5.2$, $p = .028$.

The middle panel of Figure 8 shows MT for trials with different cue validity, for Experiment 5. MTs were slightly faster for valid trials (719 ms) than for opposite trials (757 ms). Uncorrected $t(19) = .035$. No other differences among cue types were significant. Overall movement times were approximately 280 ms slower here than in Experiment 4. $F(1,39) = 45.2$, $p < .001$.

Figure 12 shows the frequency and amplitude of fixational movement in each axis, for the valid trials only, during the last 500 ms before movement onset. As was seen in previous studies, both frequency and amplitude of fixational movement in the valid trials reflected the axis of forthcoming movement. Amplitude (left panel) was greater in the axis of forthcoming voluntary movement than in the orthogonal axis. For a one-sample t-test comparing the ratio of movements in the two axes to 1, $t(20)= 5.9$, $p < .001$. Frequency (right panel) was greater in the axis orthogonal to the forthcoming move than in the main axis: $t(20) = 6.1$, $p < .001$.
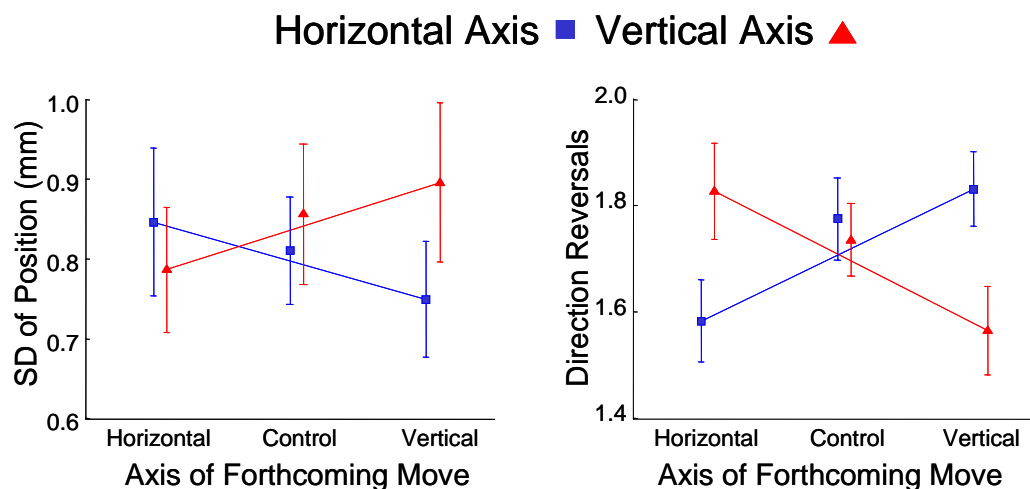
Figure 12. Amplitude and frequency effects for Experiment 5, valid trials only. Left Panel. Across participant mean (±1 SE) of standard deviation of position (mm) along the horizontal and vertical axes before target-directed movements along the horizontal (H) and vertical (V) axes. Right Panel. Mean number (±1 SE) of direction reversals in each axis, while holding still in the horizontal and vertical axes, before target-directed movements along the horizontal (H) and vertical (V) axes.

The middle panel of Figure 10 shows the influence of cue validity on the amplitude effect. In contrast to trials with valid precues, there was a significant decrease in amplitude in the axis of forthcoming movement, relative to the orthogonal axis, for trials with adjacent precues: $t(21) = 4.8$, $p < .001$. As you can see by comparing the left and middle panels of Figure 10, differences in the reciprocity of the movement being prepared interacted with cue validity for the amplitude effect, such that cue validity had greater influence on the reciprocal moves than on the discrete moves. $F(6,117) = 3.4$, $p = .020$.

The middle panel of Figure 11 shows the influence of cue validity on the frequency effect. As in trials with valid precues, there was a significant decrease in frequency in the main axis, relative to the orthogonal axis, for trials with neutral precues ($t = 3.7$, $p = .002$). A comparison of the left and middle panels of Figure 11 reveals no differences in the frequency effect as a function of the reciprocity of the movement being prepared.

Discussion

The purpose of Experiment 5 was to determine whether preparation is different before discrete and reciprocal moves. Several possible relations between reciprocal and discrete movement were proposed. One perspective holds that a discrete move is formed by planning and truncating a reciprocal move. A second perspective holds that a reciprocal move is formed by planning and concatenating two discrete moves: one to the target and one back. A third possibility is that discrete and reciprocal moves belong to two different classes such that neither is built from the other.

Experiment 5 was identical to Experiment 4, with one critical difference: in Experiment 4, all target-directed moves were reciprocal. In Experiment 5, they were discrete. Instead of moving as

quickly as possible to the peripheral target and back to the center, participants moved rapidly to the peripheral target and waited 2 s for a signal to return to the center. If reciprocal moves are concatenations of discrete moves, then reciprocal moves should be slower to initiate than discrete moves, because the planning would involve the stringing together of two discrete moves. Therefore, RTs should be faster in Experiment 5 than they were in Experiment 4. Furthermore, discrete moves should demonstrate reduced anticipatory effects relative to those seen in Experiment 4. If, on the other hand, discrete moves are truncated reciprocal moves, they should be slower to initiate than reciprocal moves, because a plan for a reciprocal move would need to be generated and then edited. Furthermore, discrete moves should show enhanced anticipatory effects relative to Experiment 4.

For a given target size and distance, a discrete move is more difficult than a cyclic move, because acceleration as well as position and velocity must be controlled. Thus, movement times to the peripheral target in Experiment 5 should be slower than in Experiment 4. This expected result was obtained, confirming that the manipulation did increase the difficulty of movement, presumably by making it less cyclic.

Typically, RT is longer when MT is longer, as for instance in the invalid conditions as compared to the valid conditions. The two measures so often correlate positively that some have gone as far as to suggest that RT is dependent on MT (Quinn, Schmidt & Zelaznik, 1980). Thus, finding slower RTs in Experiment 5 as compared to Experiment 4 would have been unsurprising. The results, however, indicated the reverse: RT was quicker before discrete movements than before reciprocal moves. These results make sense if you consider that a plan for discrete movement has only to consider one end point, while a plan for a reciprocal movement has to consider two. The results are thus inconsistent with an explanation of discrete moves as truncated reciprocal moves, and consistent with an explanation of reciprocal moves as concatenated discrete moves. The results are also consistent with an account of reciprocal and discrete moves as belonging to separate classes.

The discrete vs. reciprocal manipulation had no discernable influence on the frequency effect. It did, however, interact with cue validity in the amplitude effect. Cue validity had a smaller influence on the amplitude effect for discrete moves than for reciprocal moves. If the anticipatory effects are a measure of planning, these results suggest that reciprocal moves require more planning than discrete moves, again arguing against the perspective that discrete movements are made from truncated reciprocal moves.

Experiment 6

In all the experiments in this line of research, participants were required to hold an intended arm movement in mind while delaying execution of that movement. While waiting to move, participants may have started to drift toward the next anticipated target, then caught themselves and made a corrective movement back toward the center of the home circle. The corrective movements could be triggered by a perceptible change in the visual feedback. The *Drift and Correct* hypothesis says that the effects observed here were due to these corrective movements.

Experiment 6 investigated this hypothesis by changing the visual feedback available to participants while they waited to move.

If the effects found in these studies were caused by visually-triggered corrections, they should be sensitive to the quality of the visual feedback, in particular the visible distance between the representation of the finger and the boundary of the center circle. Thus, the larger the center target is, the farther and longer participants may drift before realizing that a corrective movement is needed, and the larger the amplitude and frequency effects would be. Conversely, a smaller center target should curtail drifting and induce more rapid corrections.

In a reciprocal move, the staging area is also the final target. This fact would confound any attempts to investigate the influence of one or the other alone. However, the discrete movements introduced in Experiment 5 made it possible to manipulate features of the staging area without affecting the final target. Experiment 6 exploited this potential to investigate the *Drift and Correct* hypothesis. The size of the center circle was reduced relative to the center circle used in Experiment 5. According to the logic laid out above, this should lead to more rapid corrections, which would in turn lead to reduced amplitude and frequency effects in Experiment 6, relative to the effects seen in Experiment 5.

It is also possible that the smaller center target would induce ironic effects. A related study found that when participants were asked to hold a pendulum and exhorted to prevent movement in one axis, the relative frequency of movement increased in that axis (Wegner et al, 1998). Along similar lines, when participants were asked to point at a target and hold as still as possible, those provided with enhanced visual feedback overcorrected, which led to greater amplitudes of fixational movement (Morrison & Keogh, 2001).

In Experiment 6, the size of the staging area was reduced in order to enhance visual feedback regarding movement error. If participants were successful at using the enhanced visual information, amplitude in the axis of forthcoming movement should decrease, and frequency should increase. If the manipulation induced ironic effects, both amplitude and frequency would be expected to increase in the axis of forthcoming movement.

The data were analyzed in two ways for this comparison. The decision to do so was based on some exploratory analyses which will be described in the Appendix.

Method

Participants

Twenty-two new participants (12 female, 10 male) were drawn from the undergraduate psychology testing pool at Penn State University. All were naïve to the study's purpose, and none had participated in any of the previous experiments in this line of work. All participants gave informed consent and filled out handedness assessments. Eighteen of the participants were right-handed, one was right-handed, and three were ambidextrous. Participants used their dominant arms for the experiment. Those who reported themselves as ambidextrous were given a choice of which arm to use after the task was described to them. Two chose to use the left arm, and one chose to use the right arm.

Procedure

The stimuli and instructions were identical to those in Experiment 5, with the exception that the diameter of the center circle was reduced to 21 cm. Peripheral targets remained the same. Data were collected, cleaned, and analyzed in the same manner as in Experiments 4 and 5. After removal of errors and outliers, each participant had an average of 202 good trials.

The data were also reanalyzed with a slightly different fixation period. Instead of defining the window of interest as the last 500 ms before movement onset, the window began 250 ms before the go cue and ended 250 ms after the go cue. Trials with RTs of less than 255 ms were excluded from the analysis. This led to the removal of two subjects' data from each group.

Results

Fixation period defined according to movement onset

The right panel of Figure 7 shows RT for trials with different cue validity in Experiment 6. As in Experiments 4 and 5, RTs were faster (318 ms) for valid trials than for neutral, opposite or adjacent trials (387, 390, and 375 ms respectively). $F(3,57) = 20.6$, $p < .001$. Compared with Experiment 5, RT was slower overall. $F(3,57) = 4.7$, $p = .037$.

The right panel of Figure 8 shows MT for trials with different cue validity for Experiment 6. MTs were significantly faster for valid trials (702 ms) than for neutral, opposite or adjacent trials (761, 757, and 760 ms respectively). $F(3,57) = 8.0$, $p < .001$. There was no difference in MT between Experiments 5 and 6. $F(1,39) = .027$, $p = .871$.

Figure 13 shows the frequency and amplitude of fixational movement in each axis, for the valid trials only, during the last 500 ms before movement onset. As was seen in previous studies, both frequency and amplitude of fixational movement in the valid trials reflected the axis of forthcoming movement. Amplitude (left panel) was greater in the axis of forthcoming voluntary movement than in the orthogonal axis. For a one-sample t-test comparing the ratio of movements in the two axes to 1.0, $t(19) = 3.3$, $p = .004$. Frequency (right panel) was greater in the axis orthogonal to the forthcoming move than in the main axis: $t(19) = 10.8$, $p < .001$.
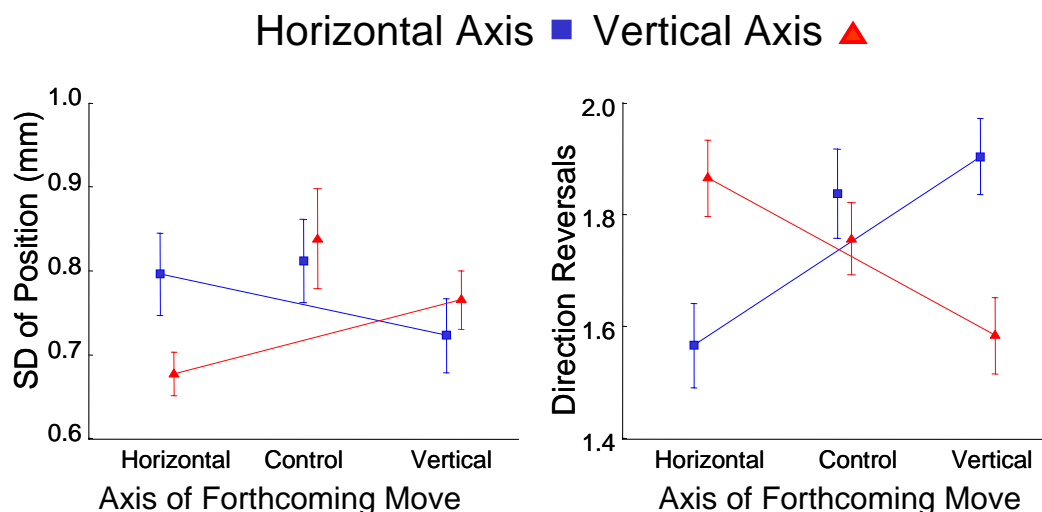
Figure 13. Amplitude and frequency effects for Experiment 6, valid trials only. Left Panel. Across participant mean (±1 SE) of standard deviation of position (mm) along the horizontal and vertical axes before target-directed movements along the horizontal (H) and vertical (V) axes. Right Panel. Mean number (±1 SE) of direction reversals in each axis, while holding still in the horizontal and vertical axes, before target-directed movements along the horizontal (H) and vertical (V) axes.

The right panel of Figure 10 shows the influence of cue validity on the amplitude effect. As for trials with valid precues, there was a significant increase in amplitude in the axis of forthcoming movement, relative to the orthogonal axis, for trials with neutral precues: $t(19) = 2.2$, $p = .037$. As you can see by comparing the middle and right panels of Figure 10, differences in the size of the center circle had no influence on amplitude effect.

The right panel of Figure 11 shows the influence of cue validity on the frequency effect. As in trials with valid precues, there was a significant decrease in frequency in the main axis, relative to the orthogonal axis, for trials with neutral precues ($t = 2.7$, $p = .013$) and for trials with opposite precues ($t = 4.1$, $p = .001$). Comparing the middle panels and right panels of Figure 11 reveals no differences in the frequency effect as a function of the size of the staging area.

Fixation period defined according to go cue

Results of the reanalysis are shown in Figures 14 and 15. Once again, there were no significant differences in frequency effect as a function of the size of the staging area. However, the size of the staging area had a significant influence on the amplitude effect in this time window. $F(1,35) = 5.1$, $p = .03$. Effects were smaller in Experiment 6, with the smaller staging area, than in Experiment 5, with the larger staging area. Cue validity still had a significant effect in both experiments. Experiment 5: $F(3,51) = 3.6$, $p = .020$; Experiment 6: $F(3,54) = 3.3$, $p = .026$.
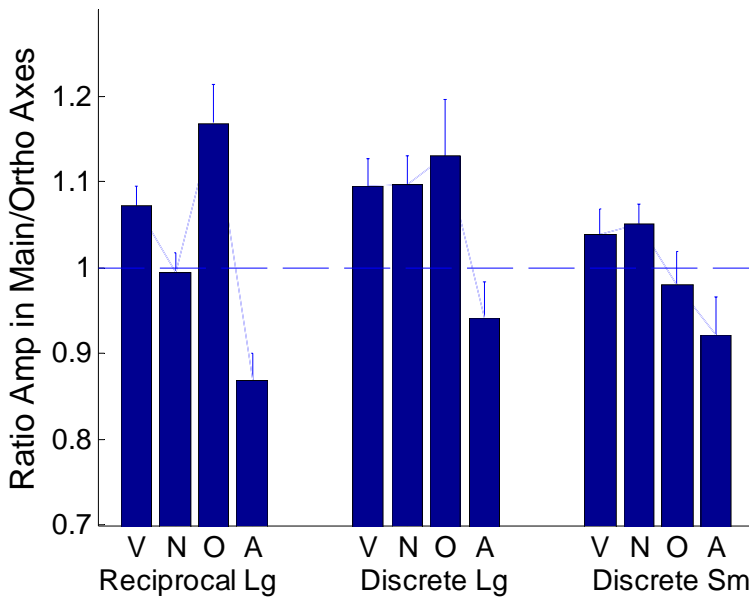
Figure 14. Amplitude effect relative to go cue. Amplitude effect expressed as a ratio of standard deviation of position in the axis of forthcoming movement to standard deviation of position in the axis orthogonal to forthcoming movement. Left panels: Experiment 4. Middle Panels: Experiment 5. Right panels: Experiment 6. Conditions: valid (V), neutral (N), opposite (O), and adjacent (A).
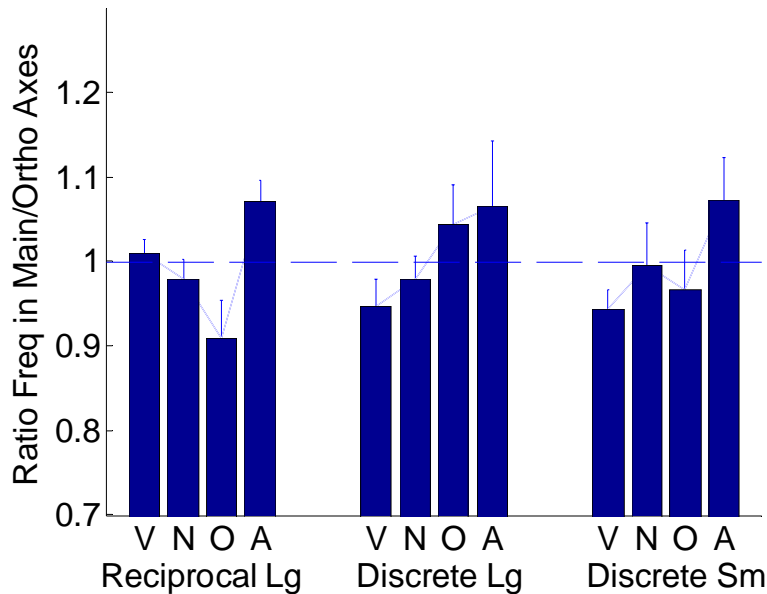
Figure 15. Frequency effect relative to go cue. Frequency effect expressed as a ratio of number of direction reversals in the axis of forthcoming movement to number of direction reversals in the orthogonal axis. Left panels: Experiment 4. Middle Panels: Experiment 5. Right panels: Experiment 6. Conditions: valid (V), neutral (N), opposite (O), and adjacent (A).

Discussion

If the effects found in these studies were caused by partial failures of inhibition followed by visually-triggered corrections, they should be sensitive to the visible distance between the representations of the finger and the boundary of the center circle. To test this prediction, in Experiment 6 the size of the circle in which participants waited before moving to the next target was reduced. If participants were able to make use of the enhanced visual information afforded by the smaller central staging area, they should have curtailed drifting sooner, which would have led to more rapid corrections. The end result of this would be smaller effects, both in amplitude and in frequency. If, on the other hand, enhanced visual information caused overcorrection (so-called "ironic effects"), both amplitude and frequency would be expected to increase in the axis of forthcoming movement. If the effects were not caused by drifting and correcting, the size of the center circle should not influence the effects.

The result was weakly supportive of the *Drift and Correct* hypothesis. There were no differences between the two experiments when the time window considered was the 500 ms before movement onset. However, when the time window considered was 250 ms before and after the go cue, the amplitude effect was smaller before movement from a small center circle than before from a large center circle. Thus, the size of the staging area did affect fixational movements before target-directed moves. This result is consistent with the hypothesis that while waiting to move, participants drifted toward the expected target and then made corrections when they saw themselves approaching the boundary of the staging area.

Note that participants were specifically instructed to point to the *center* of the center circle and to *hold still* until they heard the second cue. They were not specifically exhorted to avoid movement in the axis of forthcoming movement, nor to attend to the boundaries of the center circle. Thus, the size of the staging area may have had a more indirect effect than it might have in one of the aforementioned studies that showed "ironic effects."

Possible Functions of Fixational Movement for Voluntary Movement

This project has so far documented changes in fixational movements before voluntary movement and sought for the source of these changes. Another important question is whether changes in fixational movement aid forthcoming voluntary movement. In regard to this question, two additional hypotheses were tested using the data collected for Experiments 4-6. The first hypothesis posited that there would be a correlation between a performance measure (RT or MT) and an effect measure (amplitude or frequency effect). The second hypothesis posited that changes in fixational movement would aid in synchronizing movement onset with ongoing oscillations. The additional analyses and their results are described next.

Correlation With Performance

To investigate the idea that fixational movements facilitate subsequent target-directed movement, frequency effects and amplitude effects were tested for correlations with RT and MT, both across participants and within participants. Since RT and MT both decrease as performance improves, a negative correlation between either of these performance measures and either of the

effects would be consistent with a functional use for the effect. Conversely, a positive correlation would be consistent with the effects being counterproductive for performance.

Within Participants

The first question asked was whether, for individual participants, trials with more of the effects were faster or slower than trials with less of the effects. For each trial, the amplitude effect was quantified as before, namely, by computing the ratio of amplitude in the axis of forthcoming movement to the amplitude of amplitude in the orthogonal movement. (Because there were so few direction reversals per trial, it would not have been meaningful to calculate a single trial frequency effect). Within participants, the absolute value of the average correlation between the amplitude effect and both MT and RT was less than .01 for all three experiments. Thus, for individual participants, the amount of amplitude did not predict speed of movement.

Across Participants

The second question asked was whether participants who demonstrated more of the effects were faster or slower than participants who demonstrated less of the effects. For across-participant comparisons, participants were pooled across Experiments 4-6. This provided 59 degrees of freedom, so the critical r value for significance (2-tailed) was +-.25. Across participants, there was a correlation of -.36 between amplitude effect and movement time, indicating that the fixational movements of faster participants had greater amplitude in the axis of forthcoming movement relative to in the orthogonal axis, as compared to the slower-moving participants. No other correlations were significant.

To determine the influence of the countermove on performance, correlations between performance measures and fixational movement effects with the countermove excluded – that is, with the fixation time defined by the penultimate rather than the ultimate direction reversal in the axis of forthcoming movement – were tested. This resulted in a reduction of the correlation between MT and the amplitude effect to -.12. Thus, the countermove was largely responsible for the correlation, which suggests that the countermove facilitates faster movement times. This is in accord with what has been generally seen in sports science (Asmussen, Bonde-Petersen, & Jorgensen, 1976).

Synchronization with Voluntary Movement Onset

All the analyses reported up to this point addressed the influence of the axis of forthcoming movement on the axis of the fixational movement. However, the data might also bear on the body of work addressing the temporal relation between fixational movement and subsequent target-directed movement. As was mentioned previously, the literature linking fixational movement with voluntary movement onset refers mainly to tremor. While drift can sometimes be filtered out by detrending the raw data, small quick discrete movements cannot be easily separated from tremor. Therefore it is impossible to be sure that what is being studied is solely tremor. Furthermore, there is still disagreement among tremor researchers about the relative contributions of reflexive, central, and mechanical components of physiological tremor (Morrison & Newell, 2000; Raethjen et al, 2000; Vaillancourt & Newell, 2000). This document has mostly circumvented these issues by speaking of fixational movements more generally.

However, since researchers in this area tend to speak of tremor, this section will follow that convention, with the understanding that some of what is called tremor may actually be fixational movement of some other kind.

Evidence suggests that voluntary movement onset is timed to coincide with the most advantageous phase of the tremor cycle tremor (Goodman & Kelso, 1983; Lansing, 1957; Travis, 1929). However, this synchronization does not necessarily facilitate performance (speed) of the voluntary move (Lakie & Combs, 2000; Lansing, 1957). Researchers have suggested that in order to facilitate the synchronization of ongoing oscillation and movement initiation, the motor system might reset the phase of the tremor before a voluntary movement by lengthening the last tremor cycle (Kogan, 1978). Indirect support for this hypothesis comes from findings of bidirectional influence between larger, voluntary oscillatory arm movements and discrete movement initiation (deRugy & Sternad, 2003). However, Staude and Wolf (1998) pointed out that it is difficult to test whether tremor cycle is being lengthened before movement, because tremor cycles naturally vary in length. If movement onset occurs at a completely random time, then statistically speaking, movement onset is more likely to occur during a longer tremor cycle than during a shorter cycle simply because the longer cycle provides more opportunity. This problem is known as the waiting time paradox (Kleinrock, 1975), and it creates a need for another way to look for tremor phase resetting before voluntary movement.

Analysis

In the cuing studies reported here, participants knew that the go cue would arrive 800 ms after the precue, and they knew which direction of movement would probably be called for. The results of the analyses already reported indicated that participants prepared specifically for movement in the *axis* indicated by the precue. Another analysis was performed to determine whether participants also prepared specifically to initiate movement in a particular *direction* at a particular *time* (which could be interpreted as resetting the phase of the tremor cycle). To perform this analysis, trials with the same cue validity and direction were time locked to the go signal and averaged together, for each participant. Samples from the 500 ms time window before the go cue in one precue-go cue condition were tested for correlation with samples from 500 ms time window before the go cue in another precue-go cue condition. If participants aligned their movement so as to be in a particular phase of tremor (or moving in a particular direction) when the go cue arrived, then the average paths of fixational movement in conditions with the same precue should correlate. Conversely, the paths of fixational movements in conditions with different precues should not correlate. (Because the time period of interest here ends with the go cue, the direction of the go cue cannot have any influence on the data.) Since this question was about direction, not axis, only trials with valid and opposite precues were considered. Thus, the prediction was that paths in a valid left (left-left) condition would line up with paths in an opposite right (left-right) condition, but not with a right-right or right-left condition, and so forth.

Results

The results of this analysis are presented in Figure 16 and Table 1. Rows in bold indicate predicted positive correlations. The data from Experiment 4, where the target-directed moves were reciprocal, did not support the prediction. Positive correlations were just as likely to occur between conditions with different precues as between conditions with the same precues.

However, the data from Experiments 5 and 6, where the target-directed moves were discrete, did support the prediction. When precues were the same, correlations were positive. When precues were different, correlations were negative or extremely small. Thus, synchronization occurred before discrete moves but not before reciprocal moves.

Discussion

The purpose of this analysis was to determine whether fixational movements (including tremor) are modified during movement preparation so as to synchronize ongoing oscillations with planned voluntary movement in a particular direction. Previous research has shown that discrete movement onset occurs in phase with tremor (Goodman & Kelso, 1983; Lansing, 1957; Travis, 1929). However, it has not been clear whether the tremor was modified to synchronize with the expected movement onset or the movement onset was delayed to synchronize with the ongoing oscillation. The results reported here suggest that before discrete moves, fixational movements were altered to facilitate synchronization with movement onset. Interestingly, this synchronization was not reliable before reciprocal moves. In all previously published studies linking tremor and movement onset, the required voluntary movement was discrete. Thus, these results replicate and extend previous findings.

These results indicate that people prepare differently for reciprocal moves than for discrete moves, suggesting that the two movements are fundamentally different. Harking back to the question posed in Experiment 5, it may be more accurate to think of reciprocal moves of as truncated cyclic movements rather than as concatenated discrete moves. Thus, the results imply that people prepare differently for discrete and cyclic movements. Why should this be? Cyclic movements are usually repeated more than once, so they can normally rely on repetition to build up elastic energy and correct for small errors. Discrete movements, in contrast, are often performed just once. A single instance of a discrete move (such as a kick of a soccer ball) is likely to be higher stakes than a single cycle of a cyclic move (such as a single revolution of the pedals of a bicycle). Thus, discrete movements may normally rely more on preparation than cyclic moves do.

Although the investigation of synchronization was inspired by the debate about whether movement onset is timed to coincide with tremor phase, these results do not necessarily mean that tremor phase, per se, is being reset. It may be that another movement process is overlaid on top of existing tremor. The synchronization reported here occurred before the countermove was initiated. Perhaps the countermove is preceded by a pre-countermove that sets up the countermove to happen at the right time. Thus, it may be that previous reports of synchronization of movement onset with tremor phase were actually documenting the superposition of additional small movements onto the tremor oscillation.

Table 1: Correlations between movement paths as a function of precue and go cue. Pairs that were predicted to have positive correlations are in bold. R=Right, L=Left, U=Up, D=Down.

Experiment	conditions	correlation	conditions	correlation
	Horizontal		**Vertical**	
4	RR LL	.03	UU DD	.05
	RR LR	.17	UU DU	.24
	RR RL	**.07**	**UU UD**	**.26**
	LR RL	-.18	DU DU	.30
	LL RL	-.08	DD UD	.03
	LL LR	**.17**	**DD DU**	**.14**
5	RR LL	.18	UU DD	.18
	RR LR	.06	UU DU	-.19
	RR RL	**.34**	**UU UD**	**.50**
	LR RL	.03	DU DU	-.11
	LL RL	-.05	DD UD	.22
	LL LR	**.25**	**DD DU**	.34
6	RR LL	-.11	UU DD	-.07
	RR LR	-.18	UU DU	-.06
	RR RL	**.25**	**UU UD**	**.37**
	LR RL	.10	DU DU	-.01
	LL RL	.10	DD UD	-.05
	LL LR	**.35**	**DD DU**	**.30**
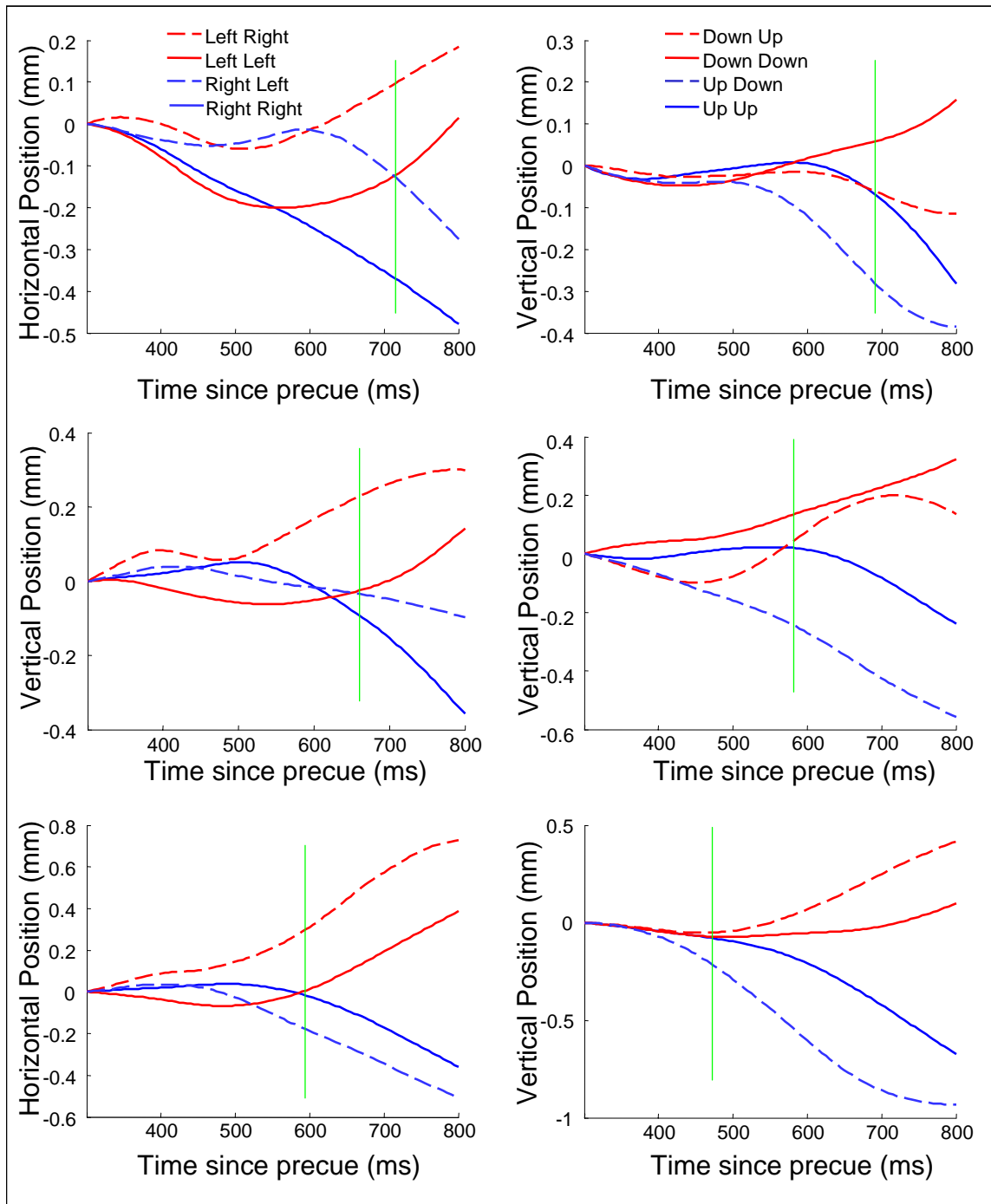
Figure 16. Average trajectories from 300 ms after the precue until the go cue. Top panels: Experiment 4, reciprocal moves. Middle panels: Experiment 5, discrete moves. Bottom panels: Experiment 6, discrete moves, small center. Green vertical lines show last crossing of lines with different precues. This occurs later for reciprocal moves than for discrete moves, and later for moves from a large circle than for moves from a small circle.

CHAPTER 4
GENERAL DISCUSSION

The purpose of this project was to investigate the relations between small movements that people make while simultaneously holding still and preparing for voluntary movements. The work builds on a long line of research investigating readiness by examining, among other measures, reaction times, brain activity levels, reflex sensitivity, and small movements that the eye makes during fixation (fixational eye movements). The new measure relies on small movements of the limb during pointing, which I call fixational limb movements. I assume that fixational movements include tremor, drift, and other components (such as quick corrections of drift). For reasons that were mostly pragmatic, I did not attempt to distinguish subtypes of fixational movements in this project, although that would be a worthy project in itself.

To use limb fixational movements as an index of readiness, I developed a series of methods in which limb position was measured while participants pointed to a central location and anticipated a target-directed movement. The approach is analogous to that used to show that fixational eye movements reflect the orientation of attention. To my knowledge, nothing like this has been done before with fixational limb movements. Previous looks at fixational limb movements have generally focused on the small movements made under instructions to continue pointing to one location (Arutyunyan & Gurfinkel, 1968; Morrison & Keough, 2001; Wegner et al, 1998). Those few studies investigating the relations between fixational movement and voluntary movement onset constrained the voluntary movement to one direction (Goodman & Kelso, 1983; Lakie & Combs, 2000; Lansing, 1957; Travis, 1929). The approach taken here allows for the comparison of fixational movements in different axes as a function of the axis of forthcoming movement.

In the six experiments reported here, the main result was consistent. During the pauses before voluntary movement, amplitudes of fixational limb movements increased in the axis of forthcoming target-directed movement relative to the orthogonal axis, while frequency of fixational limb movements showed the opposite pattern. This project investigated these fixational movement bias effects and sought to elucidate whether, and in what manner, they reflect mental and physiological aspects of readiness.

In the remaining discussion, I will summarize the results, review the possible contributors to the effects observed here, and finally point to new lines of investigation suggested by this thesis.

Summary of Results

Memorize and Perform

In Experiments 1-3, participants memorized and then performed simple sequences of pointing movements that included long pauses. This approach was chosen over one that relied on external cues to trigger the movements because movements to recalled targets were considered to be similar to self-generated movements, which have been shown to activate brain areas associated with motor preparation more strongly than do stimulus-based movements (Waszak et al, 2005).

Experiment 1 verified that the effects held across different limb segments. Experiment 2 introduced a streamlined method and several exploratory manipulations. The results indicated that the effects do not depend on the participant having previously seen the movement or having to self-generate the appropriate waiting interval. The effects are also robust to changes in visual gain and to different length pauses.

Experiment 3 tested the hypothesis that the effects are dependent on vision by asking a group of participants to perform the task both with eyes open and with eyes closed. Results indicated that the effects reflect both vision-dependent and vision-independent factors. Upon initial analysis, closing the eyes did not eliminate the effects. However, when the last submovement before movement onset was removed from the period of analysis, the story became more complex. Frequency effects were altogether absent, but amplitude effects were present in the eyes-open condition and were reversed in the eyes-closed condition. Therefore, there appear to be at least two components to the effect. One depends on the last submove and may be what is referred to in sports science as the countermove. The other depends on the availability of vision, as was further explored in Experiment 6. These results also suggested that the frequency and amplitude effects may have somewhat different origins. The frequency effect was entirely dependent on the last submove, whereas the amplitude effect was not dependent on the last submove except in the eyes-closed condition.

Cuing

Having established the robustness of the effects for movements performed from memory in the first three experiments, the next series of experiments investigated whether the effects would replicate for movements performed in response to stimuli. The cuing method implemented in Experiments 4-6 was similar to those used elsewhere in psychology, neuroscience, and kinesiology (Posner, Snyder & Davidson, 1980). Participants pointed to a central target and waited for a go signal, which was preceded by a precue. Upon hearing the go signal, participants pointed as quickly as possible to the target indicated. In Experiment 4 they returned immediately to the center circle in one fluid movement. In Experiments 5 and 6 they stopped in the target and waited for another cue to tell them to return to the center circle. The cues were auditory sound files consisting of color words that matched the four peripheral targets, as well as "stay" for control conditions and "wait" for neutral conditions.

The cuing method offers several advantages over the memorize-and-perform method. First, it gives experimenters more control over the timing and accuracy of the information participants receive about the forthcoming movement. This allows the observation of participants' behavior as they incorporate new information, as well as the measurement of reaction time, a common way to evaluate readiness. Second, the cuing method eliminates the need for the extra 'home and back' movement in between target and back moves. Rather than requiring every target-directed move to follow a move from the same home target, every direction of movement can occur after every other direction of movement an equal number of times. Third, this method provides two different baseline conditions: a control condition, in which participants know that they will not be asked to move to a target imminently, and a neutral condition, in which they know that they will be asked to move to a target, but they don't know which one.

Results from the cuing studies indicated that participants were sensitive to cue validity. Reaction times and, to a lesser degree, movement times were shorter when the precue was valid than when it was neutral or invalid. Furthermore, the frequency and amplitude effects were sensitive to cue validity. When the precue was valid or opposite (same axis, different direction) with respect to the go cue, both the frequency and amplitude effects resembled those seen in Experiments 1-3. In addition, when the precue was neutral, frequency effects resembled those seen previously. This difference suggests a dissociation between the frequency and amplitude effects. When the precue was not in the same axis as the go cue, both the frequency and amplitude effects were reversed, indicating that participants were preparing for a movement in the wrong axis. The difference between amplitude and frequency effects in the neutral condition suggests that the amplitude effect is more influenced by the precue than the frequency effect. This fits with the earlier finding that the frequency affect is more influenced by the countermove than the amplitude effect, in support of the idea that the two effects are somewhat dissociable and may have different causes.

Experiments 4-6 also established a less fatiguing relation to gravity and a balanced proportion of moves in each axis. Participants lay on a mattress on the floor and pointed at targets on the ceiling. The amplitude effects found here were more symmetrical than in Experiments 1-3, supporting the idea that fatigue influenced the fixational movements seen earlier but did not cause them or their associated effects.

Discrete vs Reciprocal Moves

The purpose of Experiment 5 was to determine whether preparation is different before discrete and reciprocal moves. More generally, Experiment 5 was designed to help cast light on the control of reciprocal moves, given that the control of such moves can be explained differently depending on whether one thinks that movements are fundamentally discrete or cyclic. Several possible relations between reciprocal and discrete movement have been proposed. One perspective holds that a discrete move is formed by planning and truncating a reciprocal move. Another perspective holds that a reciprocal move is formed by planning and concatenating two discrete moves: one to the target and one back. A third possibility is that discrete and reciprocal moves belong to two different classes, with neither built from the other.

To investigate this question, the task was modified so that, instead of moving as quickly as possible to the peripheral target and back to the center, participants moved rapidly to the peripheral target and waited 2 s for a signal to return to the center. If reciprocal moves are concatenations of discrete moves, then discrete moves should be faster to initiate than reciprocal moves, because the concatenation time is saved. However, if discrete moves are truncated reciprocal moves, discrete moves should be slower to initiate than reciprocal moves, because the editing time is added. Additionally, if the fixational limb movement bias reflects planning, then the frequency and amplitude effects should be larger in whichever condition is more complex to plan.

Both reaction times and movement times were affected by this manipulation. Movement times were significantly longer for discrete moves than for reciprocal moves. This was unsurprising, in light of the well-known fact that coming to a full stop (with velocity and acceleration both equal to zero) is more difficult than simply reversing direction. Reaction time results were more

surprising: RTs were shorter before discrete moves than before reciprocal moves. This result argues against the idea that RT is purely controlled by MT (Quinn, Schmidt & Zelaznik, 1980). Furthermore, the finding that discrete moves required less time to plan than reciprocal moves despite the longer movement time to the (first) target suggests that reciprocal moves are more complex than discrete moves (Fischman & Lim, 1991). This argues against the view that discrete movements are made from truncated reciprocal moves, although it does not distinguish between the possibility that reciprocal movements are concatenated discrete moves and the possibility that the two moves belong to separate classes.

The discrete vs. reciprocal manipulation had no discernable influence on the frequency effect. It did, however, influence the amplitude effect (again supporting a dissociation between the two effects). Cue validity had a smaller influence on the amplitude effect for discrete moves than for reciprocal moves. If the anticipatory amplitude effect is a measure of planning, the present results suggest that reciprocal moves require more planning than discrete moves, consistent with the idea that they are more complex from the nervous system's perspective, as argued above.

Brain imaging studies of discrete and cyclic movement have indicated that discrete movements activate more areas of the brain than cyclic movements do, suggesting that cyclic movements are simpler or more fundamental than discrete movements. The present finding that a single reciprocal movement requires *more* planning than a discrete movement suggests that a single reciprocal movement is very different from a series of cyclic movements. This is consistent with results of timing studies, in which the first few movements of a series were executed differently from later movements (Zelaznink, Spencer, Ivry, et al, 2005).

Influence of Staging Area Size

Experiment 6 investigated the hypothesis that participants waiting to move would begin to drift in the direction of the expected target, then catch themselves and make a corrective movement. This is similar to what has been seen in fixational eye movements (Hafed & Clark, 2002; Engbert & Kliegl, 2003; Laubrock, Engbert & Kliegl, 2005). Corrective movements could be triggered by a perceptible change in the visual feedback such as the distance between the visual representation of the finger and the boundary of the center circle. To test this, a smaller center target was presented as the staging area where participants wait before pointing to the peripheral targets. The target-directed moves were discrete rather than reciprocal, so that the staging area did not also serve as a target and thus confound the results. If the drift-and-correct hypothesis is correct, and if participants were able to make use of the more precise information provided by the smaller center circle, this manipulation should curtail drifting and induce more rapid corrections during the waiting period, resulting in smaller anticipatory effects, both in amplitude and in frequency.

RT was larger for movements from a small circle than for movements from a larger circle. This was a surprising finding. Previous studies have shown an effect of target size on RT when moving back and forth between targets (Adam and Paas, 1996), and numerous studies have shown that participants move more slowly to a small target than to a large one (Fitts, 1954; Woodworth, 1899) but this is to my knowledge the first study showing that reducing the size of the staging area alone increases RT. The novelty of the finding (assuming it is novel) may come

from the novelty of the task, since experimental investigations of limb movement typically start with the arm supported, rather than held as motionless as possible in the air.

Although the frequency and amplitude effects in the two axes in the last 500 ms before movement onset were not significantly influenced by the change in size of staging area, there was a concern that a difference in effects may have been obscured by the difference in RT. Therefore, the data were reconsidered with the window of interest defined according to the stimulus (250 ms before and after the go cue) rather than to movement onset. This analysis suggested that the amplitude effect was reduced when the staging area size was reduced. This result is consistent with the drift-and-correct hypothesis.

Countermoves Facilitate Speed

If fixational movements facilitate subsequent target-directed movement, there might be a correlation between either the amplitude effect or the frequency effect and either RT or MT, either within or across participants. There was no correlation between any of these measures within participants. However across participants there was a significant correlation between amplitude effect and movement time, indicating that the fixational movements of faster participants had greater amplitude in the axis of forthcoming movement relative to in the orthogonal axis, as compared to the slower-moving participants. This correlation was only significant when the countermove was included in the analysis window, suggesting that the countermove facilitates faster movement times. This fits with previous research showing that countermovements improve the power of ballistic actions (Asmussen, Bonde-Petersen, & Jorgensen, 1976).

Synchronization

To determine whether participants prepared specifically to initiate movement in a particular direction at a particular time, position data from trials with the same cue validity and direction were time-locked to the go signal and averaged together, then compared to averaged trials with different cue validity and direction. If participants aligned their movements so as to be in a particular phase of oscillation when the go cue arrived, then the average path of fixational movement in conditions with the same precue should align, as reflected by a positive correlation. Conversely, the paths of fixational movements in conditions with precues indicating opposite directions should not align. Thus, paths in a valid left (left-left) condition would line up with paths in an opposite right (left-right) condition, but not with a right-right or right-left condition, and so forth.

The results offered support for the hypothesis and shed further light on the relation between discrete and reciprocal movements. When participants waited to perform discrete movements, movement paths showed strong alignment depending on the precue. However, when participants waited to perform reciprocal movements, movement paths did not show particular alignment depending on the precue. Thus, synchronization occurred before clearly before discrete moves than before reciprocal moves. These results suggest that people prepare differently for reciprocal moves than for discrete moves, suggesting that the two movements are fundamentally different. While the differences in RT and amplitude effects between discrete and reciprocal moves

suggested that reciprocal moves require more planning than discrete moves, the present results paint a more complex picture.

Although the investigation of synchronization was inspired by the debate about whether movement onset is timed to coincide with tremor phase, these results do not necessarily mean that tremor phase, per se, is being reset. It may be that another movement process is superimposed on existing tremor. The synchronization reported here occurred before the countermove was initiated. Perhaps the countermove is preceded by a pre-countermove that sets up the countermove to happen at the right time. Then, if the cue turns out to have been misinformative, another quick movement is inserted.

A closer look at the results provides support for this hypothesis. Figure 17 shows a timeline of average trials with valid and opposite precues (called valid and opposite trials here). Note that the countermove for the valid trial occurs just 30 ms after the go cue. Because of the time it takes for a motor command to travel from the brain to the muscles, we can assume that the command to initiate this movement must have been sent before the go cue was perceived and processed, and thus before it was known whether the trial was valid or invalid. Therefore a pre-countermove is shown for the corresponding opposite trial. This is followed by a very quick reversal, in order to insert a new countermove before movement onset. At the moment the countermove begins, the opposite trial is 140 ms behind the valid trial. Then the countermove for the opposite trial is cut short, such that by the time of movement onset the opposite trial is only 70 ms behind the valid trial. However, by the time of the direction reversal at the target, the ground gained by shortening the countermove has been lost. The valid trial is 140 ms faster than the opposite trial. Thus, cutting the countermove short seems to lead to slower movement. This supports the argument that the countermove facilitates fast performance. It also illustrates the potential advantage of synchronizing fixational movement with the expected time and direction of the go cue.

	Go Cue			
Valid	CM		RT	MT
	30		310	740
Time (ms)	30	170	380	880
Opposite	PCM	CM	RT	MT

Figure 17. Timeline of pre-countermove (PCM), countermove (CM), movement onset (RT), and reversal at target (MT) for an average trial with a valid precue (top) and an average trial with an opposite precue (bottom).

Other Possible Relations

In addition to the hypotheses specifically tested for this project, there are other ways that fixational movements, or changes in fixational movements, could contribute to movement preparation. Three possibilities will be described below. They are tuning proprioception,

attenuating postural reflexes, and preventing unwanted movement. None of them are mutually exclusive. Changes in fixational movements could reflect any or all three of these processes.

Tuning Proprioception

The results of numerous investigations attest to the importance of the initial posture in determining the final posture in a reaching movement (Desmurget, Gréa, & Prablanc, 1998; Hermens & Gielen, 2004; Sainburg, Lateiner, Latash, & Bagesteiro, 2003). In order to take the initial posture into account in planning a movement, the system has to know where that initial posture is. Vision of the limb's starting position has an influence on movement accuracy (Brown, Rosenbaum & Sainburg, 2003; Paillard & Brouchon, 1968; Vindras, Desmurget, Prablanc, & Viviani, 1998; Wann & Ibrahim 1993). However, proprioception is also important. People with normal proprioception and vision are able to move with only moderately reduced accuracy when vision is unavailable, whereas people without proprioception have difficulty controlling their movements even with the aid of vision (Gordon, Ghilardi, & Ghez, 1995; Rossetti, Desmurget, & Prablanc, 1995). Proprioceptive information comes from receptors in the muscles, some of which are sensitive to position and some of which are sensitive to velocity. Therefore, in order to have the most accurate information possible about the location of a limb, it may be useful to be in motion. Thus, the addition or enhancement of small movements during posture could serve to enhance sensory input available to the muscle spindles, which would in turn assist with the generation of accurately scaled motor commands.

While the idea that fixational movement is "for" proprioception might seem far-fetched, it is consistent with neuropsychological evidence that tremor is increased in many patients with reduced proprioception (Anouti & Koller, 1995; Cardoso & Jankovic, 1993; Klawans, 1987). This is what one might expect if patients were compensating for the loss of proprioception by increasing movement. The enhancement of fixational movements in patients suggests a way to test the idea presented above. If fixational movements are increased in the axis of forthcoming movement in order to enhance proprioception, the effects should be greater in patients with decreased proprioception than in healthy controls.

Attenuating Postural Reflexes

During maintenance of a posture, postural reflexes are set to resist movement (Denny-Brown, 1929). Theoretically, this could be a problem for movement, because postural reflexes that serve to maintain a posture against perturbation should also prevent movement initiation. Proponents of the equilibrium point hypothesis call this "Von Holst's paradox" (Feldman & Latash, 2005). They claim that it sheds light on a fatal flaw in models of motor control in which posture and movement are controlled separately, and that it demands a model in which movement is controlled entirely by way of posture. However, another possibility is that postural reflexes are attenuated immediately preceding movement. This hypothesis is consistent with findings that inhibition of muscles that are antagonists to a movement occurs before activation of the agonists (Hufschmidt & Hufschmidt, 1954). It is also consistent with the large body of literature supporting the separate control of posture and movement (Brown, Rosenbaum & Sainburg, 2003; Kurtzer, Herter, & Scott, 2005).

If there is a transitional period before movement during which postural reflexes are attenuated, this could lead to increased compliance in the direction of forthcoming movement. Thus, the amplitude of fixational movements would increase in the axis of forthcoming movement. The results reported here are consistent with this hypothesis.

Preventing Unwanted Movement

Changes in fixational movement might also reflect attempts by the system to prevent movement in undesired directions. Recent research suggests that the motor system is capable of selectively stiffening to prevent movements in particular directions. For example, Burdet, Osu, Franklin, and Kawato (2001) asked participants to repeatedly make straight movements to targets through an unstable force field that amplified errors in proportion to their magnitude. Over time, participants learned to resist the force field and make straight target-directed movements. The researchers concluded that the motor system selectively adapted stiffness in the limb. Franklin, Liaw, Milner, Osu, Burdet, and Kawato (2007) replicated these results and also applied random perturbations to the well-learned movements to determine stiffness in different directions. They found that resistance to perturbations was greatest in the axis orthogonal to the intended movement, as would be expected if participants could selectively stiffen their muscles in an adaptive fashion. Darainy, Towhidkhah, and Ostry (2007) found similar directionally-specific resistance to perturbation during movements without the addition of a destabilizing force field. These findings of directionally specific resistance to perturbation could indicate that stiffness increases, or they could reflect the tuning of reflexes – both stretch reflexes and long-loop reflexes – to respond to perturbations (Popescu, Hidler, & Rymer, 2003). Either way, they indicate functional tuning to prevent movement in undesired directions.

All of the studies described above investigated changes during movement; none addressed the period before movement began. Stiffness during posture is associated with increased tremor frequency (Morrison & Newell, 2001). Thus, if preparation for a voluntary movement includes safeguards against moving in undesired directions, the frequency of fixational movements in the axis orthogonal to the intended forthcoming movement should increase relative to the frequency in the axis of intended movement. The frequency effects reported here are consistent with this hypothesis. It is unclear whether the amplitude effects are consistent with a stiffness explanation or not. Reports are mixed as to whether increasing stiffness increases or decreases amplitude of fixational movement (Morrison & Newell, 2001).

Changes in fixational movement prior to voluntary movement are of interest for the role(s) they may play in preparation, as described above. In addition, they are of interest for the insights they may provide into cognitive processes. The next section explains why this is important.

Cognition and Readiness

The research presented here bears on the classical problem of the relation between thought and action. This problem has fascinated psychologists since the earliest days of the field. Among the variety of answers posited, a broad distinction has been made between the idea that thought and action are essentially separate and the idea that they are essentially connected. One type of model

– the serial processing model -- is more naturally associated with the former idea, whereas another type of model – the cascade processing model -- is more naturally associated with the latter idea.

In the nineteenth century, Donders (1868/1969) developed a subtractive method for measuring the stages of cognition. According to his method, the time to complete a simple task (such as a simple RT task) was subtracted from the time required to complete a more complex task (such as a choice RT task). The difference was supposed to be a measure of the amount of time required for the additional stage(s) in the more complex task. This method relied on the assumption that perception, cognition, and action take place in discrete stages, in which each process must be completed in succession in order for the next process to begin. In contrast, James (1890) and Carpenter (1884) believed that thought and movement were inextricably intertwined and even simultaneous. Carpenter coined the term "ideomotor" to describe this simultaneity.

More than a century later the two perspectives are still being debated. Some psychologists have advocated discrete stage models of processing in which the output of a stage of processing is not available for the next stage of processing until it is complete (Sternberg, 1969, 1975). Others have advocated continuous models, in which information from one processing stage is passed along to the next stage before it is completely processed (Eriksen & Schultz, 1979; Greenwald, 1970; McClelland, 1979). The last several decades have seen a gradual erosion of support for pure stage models for early stages of processing, in part because of evidence from neuroscience. For instance, single cell recordings in monkeys demonstrated transmission of information to motor cortex before all information for movement selection was available (Requin & Riehle, 1995). However, stage models retain their appeal in part because their assumptions allow researchers to make and test stronger predictions (Sanders, 1990). In addition, support remains for intermediary models, with smaller discrete sub-stages (Miller, 1993). Some researchers remain convinced that although continuous models are plausible for perception, they do not apply to action (Gottsdanker & Shragg, 1985; Gazzaniga, Ivry & Mangun, 1998). Evidence supporting this perspective can be found in the brain. The basal ganglia are thought to act as gatekeeper, sending tonic inhibitory signals to the thalamus that prevent movement until a threshold is crossed. So-called omnipause neurons are thought to serve a similar function for the visual motor system (DeLong, 1990; Fuchs, Kaneko, &Scudder, 1985).

Despite the aforementioned resistance to the idea of cascading activation in the motor system, evidence in favor of the idea is beginning to mount. Eye movements are a good way to study this question, because they are fairly simple compared to limb movements, and because the neural pathways underlying them are better understood. Recent studies indicate that microsaccades reflect either the orientation of covert attention (Hafed & Clark, 2002; Engbert & Kliegl, 2002; Laubrock, Engbert, Rolfs & Kliegl, 2007) or oculo-motor preparation (Horowitz et al, 2007). The argument may be moot, however, as evidence suggests that anticipatory attention and motor preparation are organized in similar ways (Brunia, 1999). Either way, the bias in these tiny eye movements seems to indicate that some activation leaks through in advance of a clear decision to move, suggesting that the gate is not as solid as a simple threshold model might suggest.

The theory of event coding has emerged as an important contributor to the conversation. Its core claim is that anticipating a perceptual event and planning an action are conceptually and functionally equivalent, so that voluntary actions may come into being by anticipating their distal

effects (Hommel, Musseler, Aschersleben, & Prinz, 2001). Thus, the theory is compatible with a view of perception and action as overlapping processes rather than discrete stages. Evidence for the theory comes from studies of stimulus-response compatibility (Eimer, Hommel, & Prinz, 1995; Knuf, Aschersleben, & Prinz, 2001) and from the discovery of cortical areas that appear to code both for actions and for their anticipated consequences (Elsner et al, 2002).

New technologies for observing the brain in action have led to renewed interest in the neural similarity between real and imagined movements. Evidence suggests that the two phenomena have much in common. Studies of the pre-supplementary motor area suggest that it plays much the same role in representing observed, imagined, and intended actions (Cunnington, Windischberger, & Moser, 2005). Theoretically, it would be possible for a solid barrier to prevent the leakage of imagined movements into execution systems, but this does not seem to be the case. Neural evidence indicates that inhibition of prepared saccades happens at multiple levels, not in a single all-or-none fashion (Berthoz, 1996). Furthermore, merely imagining a leg movement can cause modulation of spinal reflexes (Bonnet, Decety, Jeannerod, & Requin, 1997). Therefore, the similarity of imagined and planned movements provides evidence in support of continuous activation all the way through the motor system.

Another front line of this battle is language. The production of speech errors suggests that we often begin speaking before we have finished formulating the word we need to say. Laboratory studies also support the idea that speech processing is continuous. Balota and Abrams (1995) demonstrated that factors known to influence reaction time in language studies (such as word frequency) also affect the kinematics of responses in a manual task. This result would not have been expected if the motor system could not act until "higher" systems had completed their processing. Spivey, Grosjean & Knoblich (2005) also examined kinematics of a manual response to demonstrate continuous processing of speech. Their participants made arm movements while listening to words and deciding which picture they named. The researchers claimed that the curved path of the hand movement not only reflected continuous processing, but projected it into visible space. This claim may be overstated in light of other possible explanations for curved hand paths (van der Wel et al, in press). However, the data add to the growing body of evidence that the motor system can act before decisions have been finalized.

The results presented here demonstrate that fixational movements – including tremor and other small movements taking place during ostensive stillness in a pointing task – reflect online processing of cues and decisions about which direction to move next. This finding is generally consistent with theories of cascading activation that include continuous flow all the way through the motor system.

Limitations and Next Steps

All methods have limitations, and those used here are no exceptions. It is useful to list these limitations here, especially to help chart a course for future investigations. This view to the future defines the theme of this section.

Regarding limitations, the measurement methods used were extremely simple. A choice was made to avoid the highly technical analysis methods that are sometimes used for advanced signal processing. Over the course of the studies, a picture emerged suggesting that the effects probably do not reflect changes in tremor per se. Thus, the usefulness of methods assuming an oscillatory signal (such as wavelet analysis) is questionable. However it is conceivable that some more elaborate measures could pick up more subtle differences in effects.

Some of the disadvantages of the method used in the initial studies were worked out in the later studies. For instance, while asking participants to time their own pauses seemed reasonable, it proved too difficult for many of the participants and was eliminated after the first study. Second, the home-and-back moves and the need to hold the limb up against gravity created imbalances in the activity levels across different muscles in the arms. Third, the early studies collected very little data from each participant, in part because the method was time consuming and fatiguing. Fourth, the early methods did not allow experimenters to control when the information about the next target was available to participants. All of these faults were corrected in the cuing version of the method.

Experiments 4-6 made comparisons across groups of participants. Some of the results were marginally significant and would potentially be improved by a within-participants design. To make this possible, the number of trials in each condition would need to be modified to allow the collection of sufficient data in each condition without fatiguing participants.

Drift

A potential confound for the comparisons made across experiments 4-6 was the possibility that participants drifted toward the target during the waiting time. To evaluate the role of drift in the fixational movements observed here, the straight-line Euclidean distance between the location of the fingertip at the time of the go cue and at the time of the precue was computed for valid and control trials. The average distances for valid trials in Experiments 4, 5, and 6 were 1.4, 1.7, and 1.5 mm respectively. There were no significant differences between experiments or between valid and control conditions. Distance was also computed between the location of the fingertip 500 ms before movement onset and at movement onset. The average distances for valid trials in Experiments 4, 5, and 6 were 1.3, 1.2, and 1.2 mm respectively. There were no differences across experiments or between valid and control conditions. While this is not an iron-clad argument, it does suggest that drift did not play a major role in the results presented here.

Movement Distances

Another possible confound was the movement distance. Participants were instructed to move between centers of the circles, which were the same distance apart in Experiments 4-6. However, it is possible that the difference in center circle sizes between Experiments 5 and 6, or the different instructions between Experiments 4 and 5, caused the target-directed movement to be of different lengths. To test this, the average straight-line distances of the movement from the center circle to the target circle was computed for each experiment. The distances in Experiments 5 and 6 were not significantly different ($p = .32$). Thus, the size of the center circle did not affect the movement distance. Interestingly, though, there was a significant difference between the distances moved in experiments 4 and 5, with the reciprocal movement in Experiment 4

measuring 172 mm and the discrete movements in Experiment 5 measuring 195 mm: t(39)=4.5, p<.001. Overshooting is commonly seen in discrete movements to targets, and it makes sense that the tendency to overshoot would be reduced for reciprocal moves, because overshooting in the initial move would lead to a larger required return move. Thus, the differences between the results of Experiments 4 and 5 could conceivably be due, at least in part, to these distance disparities.

Knowledge of Start Time

In all the experiments presented here, participants knew how long they would be waiting before moving. The results of the synchronization analysis suggest that participants planned for a countermove at a particular time. If this is indeed the case, then substituting a variable SOA for the known SOA should eliminate the synchronization effects. Since the frequency effect was less influenced by cue validity than the amplitude effect was, it should remain strong in the face of an unknown SOA. The amplitude effect, however, might be expected to diminish.

Stiffness

The role of fixational movements in preparation for voluntary movement may be closely linked to the roles of tone and stiffness during readiness. Stiffness is generally studied by applying perturbations to the arm and measuring the resulting amount of displacement. This method has been applied during movement and during stillness but not during stillness immediately preceding movement. The results reported here indicate that such an experiment holds promise.

Vision

Experiment 3 revealed that vision affects the amplitude of fixational movements prior to the countermove. The explanation supported by the results of experiment 6 was that participants drifted toward the target and then corrected based on visual feedback. However, the eyes may play multiple roles. It is possible that participants look at the expected target, and this looking "pulls" the limb in the direction of the target. Numerous studies have shown that eye movements tend to lead hand movements (e.g., Abrams, Meyer, & Kornblum, 1990; Herman, Herman, & Maulucci, 1981; Reina & Schwartz, 2003). Therefore, it is reasonable to suppose that looking back and forth between current and intended target locations could lead to small arm movements in the same axis. To investigate this possibility, an eye tracker could be used.

The combination of eye tracking and fixational limb movement tracking would open up other interesting possibilities, as well. For instance, if participants were instructed to keep both the eye and the limb still, but something happened to capture their attention, would the limb prove more or less responsive to this capture of attention than the eye? Similarly, would the effects would be more or less sensitive to cognitive features of interest than eye movements? Depending on the answer, this method may prove a useful addition to the set of tools for investigating online processing during a cognitive task.

Other Variations

Two different types of movements were explored here: memorized movement sequences and cued movements. Other variations could open doors to allow the method to be applied to other

questions. One variation might be to require participants to choose their direction of movement. Differences in fixational movement before freely chosen, memorized and cued voluntary movements could contribute to the ongoing conversation about the differences in planning the different types of movements (Keller & Heckhausen, 1990; Praamstra et al, 1995; Waszak et al, 2005).

Another variation would be to supply information about the forthcoming movement in pieces. Reaction times indicate that the system can begin to plan actions before all the information is available (Rosenbaum, 1980). Biases in fixational movement could reveal whether such action planning is leaking all the way through to the motor system, and whether different kinds of partial information lead to different kinds of changes in fixational movement.

A New Area of Study

The results of these experiments suggest that the study of small fixational limb movements holds promise as a topic of investigation within the fields of motor control and cognitive neuroscience. An important step to make this possible will be to develop algorithms to distinguish among different subtypes of fixational movements. In the field of fixational eye movements, a velocity-based algorithm is used for distinguishing microsaccades from tremor and drift (Engert & Kliegl, 2003). Because of the larger role of inertia in limb movements, this algorithm may not successfully translate to limb movements, but other methods could be developed. Perhaps inspiration could be taken from work that has been done to decompose postural sway into different components (Zatsiorsky & Duarte, 1999).

Summary & Conclusion

Consistently in this series of studies, the amplitude of small "fixational" movements measured while participants waited to move increased in the axis of forthcoming movement relative to the orthogonal axis, and the frequency showed the reverse pattern. There are a number of plausible functions for this pattern of effects. The results of analyses conducted here support the hypothesis that the countermove facilitates movement speed, and the hypothesis that before the countermove, one or more movements set the system so the countermove can occur at an advantageous time. In addition, the effects are consistent with the hypothesis that postural reflexes are attenuated immediately before movement, and with the hypothesis that reflexes are tuned to restrict movement in the axis orthogonal to forthcoming movement. The effects are also consistent with the hypothesis that participants increase small movement in the axis of forthcoming target-directed movement to improve proprioceptive information. These hypotheses are not mutually exclusive.

Changes in fixational limb movements before the onset of target-directed moves appear to serve movement preparation. The countermove – a single movement away from the target just before movement onset – plays a role in increasing movement speed. Before the countermove, adjustments to orientation and oscillation phase facilitate movement onset at the expected time and in the expected direction. The latter pattern was seen more clearly before discrete moves than before reciprocal moves, indicating that the two types of movement are prepared differently.

In addition to serving movement preparation, fixational limb movements appear to reflect cognition in ways that are not directly functional. For instance, the results here support the hypothesis that participants drift toward an intended target and then correct that movement. Overall, the results are consistent with a growing body of evidence in support of cascading neural activity that flows all the way to the motor system.

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APPENDIX
TIME COURSE OF EFFECTS

In the first three experiments reported here, participants performed sequences of previously memorized movements. There were no externally provided cues, so the windows of interest had to be defined with respect to the kinematics of the movement. In the last three experiments reported here, participants moved in response to auditory cues. This opened up the possibility of defining the window of interest with respect to the cues. Given the variable amount of time between the go cue and the movement onset, it was plausible that the effects would be different when the window of interest was defined differently. The analysis described here was exploratory. The results inspired the second analysis presented in Experiment 6, in which the window of interest was defined according to the go cue rather than according to the moment of movement onset.

Figure 18 shows the time course of the effects, across all three cuing studies, for valid trials only, in five time windows. The top panels show the effects in 200 ms time windows with respect to the movement onset. The first window includes the data from 1000-800 ms before movement onset, the second window includes the data from 800-600 ms before movement onset, and so on. As was described in the results sections of Experiments 5 and 6, there was a difference in amplitude effect between the reciprocal and discrete experiments, but no difference in either effect between the small and large staging areas.

The bottom panels of Figure 18 show the effects in 200 ms time windows defined with respect to the go cue. The first window includes the data from 600-400 ms before the go cue (thus, 200-400 ms after the precue), the second window includes the data from 400-200 ms before the go cue, and so on. The last two windows include data from after the go cue. For each window, trials with movement onset during or before that window were excluded from analysis. When the data were considered this way, there was a difference between the large and small staging areas in amplitude effects, and a hint of a difference in frequency effects. This visual representation inspired the second analysis presented in Experiment 6, in which the window of interest was defined according to the go cue rather than according to the moment of movement onset.

As is evident by the time when the lines diverge from the null effects line, the amplitude effect starts about 200 ms earlier than the frequency effect. This difference suggests that the two effects may have different origins.
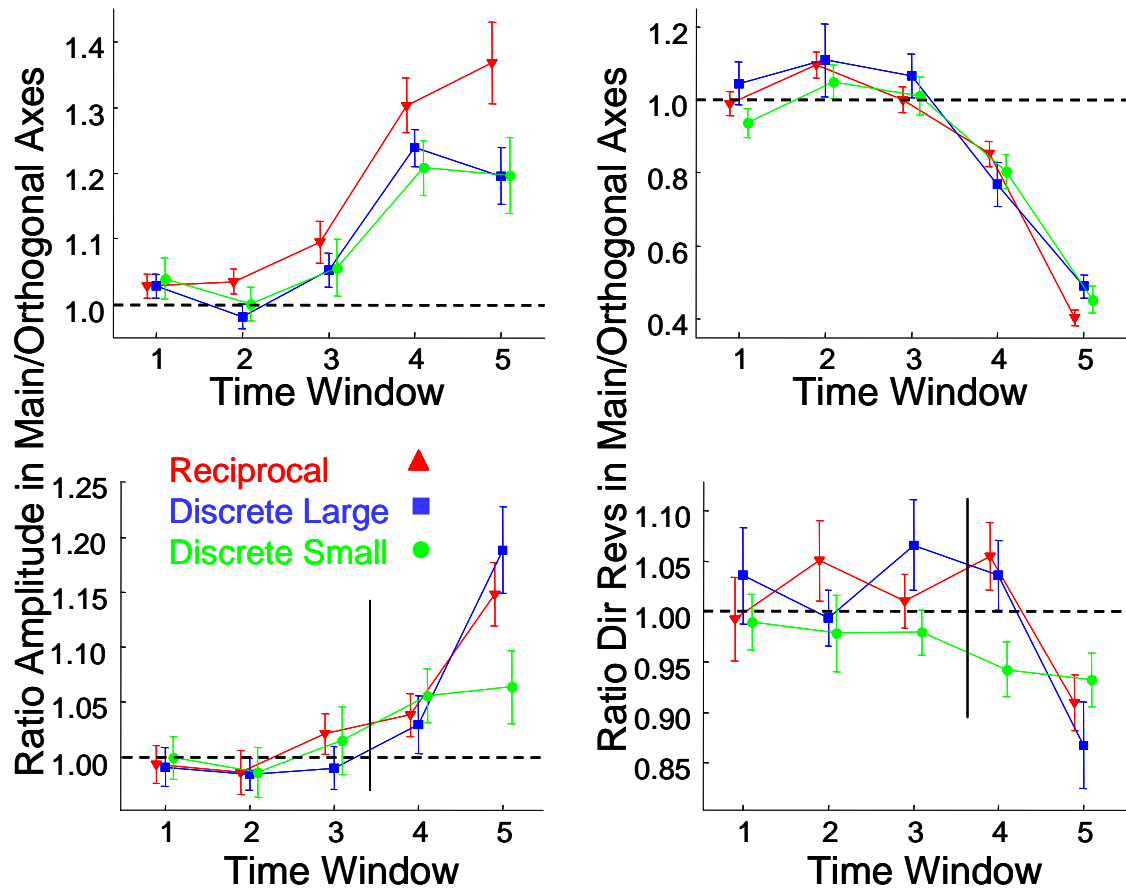
Figure 18. Time course of amplitude and frequency effects during 200 ms windows, for valid trials only. Top panels: window of interest defined with respect to movement onset. Bottom panels: window of interest defined with respect to the go cue (short vertical line). Left panel: amplitude effect. Right panel: frequency effect. Red triangles: Experiment 4. Blue squares: Experiment 5. Green circles: Experiment 6. The dashed horizontal line indicates where null results would lie.

RAJAL G. COHEN
CURRICULUM VITAE, JULY 2008

Education

Pennsylvania State University, State College, PA   Ph.D. expected August 2008
Pennsylvania State University, State College, PA   M.S.   awarded May 2005
Wesleyan University, Middletown, CT   B.A.   awarded May 2002

Awards

Post-Doctoral Training Fellowship, Neurological Sciences Institute, OHSU   2008-2010
Penn State RGSO Travel Award to European Workshop on Movement Science   2007
CMU Young Scientist Travel Award to Carnegie Symposium on Cognition   2006
Penn State Psychology Department Travel Award to Psychonomics   2004
Penn State University Graduate Fellowship   2002-2005
Wesleyan University A.L. Brown Scholarship   1989-1990
Wesleyan University Johnston Trust Scholarship   1987-1990

Publications

Cohen, R.G. & Sternad, D. (accepted). Multiple routes to improvement: Minimizing effects of neural noise on performance by exploiting redundancy and tolerance in the task space. *Experimental Brain Research.*

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