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Doing and Time:

Visuomotor Adaptations to Temporal Misalignment

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Supervisors:
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Abstract

A range of approaches to studying temporal visuomotor adaptation, grounded in the literature on spatial misalignment, has been examined. Where the visuomotor misalignment was sufficiently small, and the stimulus sufficiently predictable, this has resulted in behavioural, but not perceptual adaptation to temporal misalignment in visuomotor coordination tasks. This is in contrast to findings in the spatial literature, and in the temporal literature for intersensory and visuomotor non-coordination tasks. A possible reason for this discrepancy is that time-critical visuomotor coordination behaviour may rely on representations dissociable from those more processed representations available for retrospective judgments.

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Chapter 0: Perceiving the Past, Acting in the Future

> "Time is not a line but a dimension, like the dimensions of space.
>
> If you can bend space you can bend time also [...]."
>
> Margaret Atwood - *Cat's Eye*

When interacting with an object, one needs to detect spatial and temporal features of its behaviour, and respond with spatiotemporally appropriate behaviour of one's own. For example, if attempting to squash a resting mosquito, one must use visual information about the mosquito's location to choose the appropriate muscle activity to effect a squashing action in the correct location. If the mosquito is in motion relative to oneself, one must also make the squashing action at the correct time for the chosen location. To effectively perceive and interact with a moving object, the spatial and temporal characteristics of one's behaviour must accurately reflect those required to achieve the desired effect on the object.

The ability to choose appropriate motor actions for interacting with a moving object depends on being able to represent locations and timings in coordinate systems that are commensurate among the sensorimotor systems involved. Because the eyes are not located in the same place as the hand, spatial transformations are needed to determine where, relative to the hand, the mosquito is, given where its image impinges on the retina, and given the angles of rotation of the eyes, neck, shoulder, elbow and wrist, and the distances between each of them (Redding & Wallace, 1997a).

If the mosquito is in motion, temporal transformations are also needed. If the currently available sensory information appears to indicate that the mosquito is straight ahead and moving to the right, this information actually indicates that the mosquito was straight ahead a while ago (as sensory neural transmission is not instantaneous, e.g. Johnson, 1989). And if a motor command is sent now, the squashing action will be completed a while into the future (again, motor neural transmission takes time, e.g. Lang et al., 1985; as does the action of the muscles). One is always perceiving the past, while acting in the future; and so one must transform information about an object's location in visual time (the recent past) into an estimate of its location in motor time (the near future), if one is to time an action appropriately.

So, because sensorimotor systems are not located in the same place, nor do they experience events at the same time, spatial and temporal transformations are needed if their sensory data are to be combined, their motor actions coordinated or their actions guided by their perceptions. A fixed compensation for the spatial separation of sensorimotor systems would be ineffective. The ideal parameters for the spatial transformations do not remain constant, rather they change over a human's lifespan as the limbs grow and the distances among sensorimotor systems change (Visser, Geuze, & Kalverboer, 1998). Thus, a different combination of arm angles (and thus of muscle contractions and extensions) would be required to reach a given visual target in adulthood, compared with infancy. A failure to compensate for these changes would result in over-reaching for objects as if one's arms were the same length that they were in infancy.

Nor would a fixed compensation for the temporal separation of sensorimotor systems suffice. The relative neural processing times of various modalities change during the life-span. Allison, Wood and Goff (1983) found, in human participants, significant age-related changes in latency in a range of early evoked potentials for stimuli in visual, auditory and somatosensory modalities: From 4 to 19 years old, the latencies reduced while, from 60 to 90 years old, the latencies increased. Johnson (1989) demonstrated modality-specific age-related changes in the latency of the N100 components in humans between the ages of 7 and 20 years. Latency in the visual modality decreased with age, while the auditory component remained constant.

This thesis addresses whether and how humans can flexibly adapt their behaviour and their perception in response to experimentally induced changes in the perceived temporal separation between their eyes and their muscles. There is a great body of work on the behavioural and perceptual responses to spatial misalignment, and I use this literature to guide my investigation. In the remainder of this chapter, I define some terminology, review the literature on spatial sensorimotor adaptation and the evidence for behavioural and perceptual processes therein, discuss recent work on temporal adaptation, and indicate available routes to assessing whether similar behavioural and perceptual processes serve temporal adaptation. Finally, I set out which of those routes are taken in the present work, and outline the empirical work and arguments that follow.

Definitions

In this work, I adopt terms used in the literature on adaptation to spatial misalignment and extend them to the present work on temporal misalignment. There exist some ambiguities of terminology across different authors. For example, *calibration*, for Zwiers, Opstal, and Paige (2003), refers to the maintenance of veridical cross-sensory perception. In contrast, for Redding and Wallace (1997a), *alignment* refers to the maintenance of accurate perceptual integration in the face of mislocalization due to consistent changes in the relationship among sensorimotor systems, with *calibration* reserved for strategic motor control processes involved in responding to the more rapidly changing localization errors produced by task-related movement. In light of these inconsistencies in terminology in the literature, I outline in this section how I use certain terms.

Perceptual learning is distinguished from *world learning* in line with Bedford's (1993) definitions. World learning involves learning about one's environment through one's sensory systems, whereas *perceptual learning* involves improving the accuracy or precision of one's sensory systems, the better to apprehend and interact with the environment. World learning includes explicit memory, instrumental conditioning and classical conditioning. Perceptual learning includes discrimination learning, the McCollough effect, and the entraining of circadian rhythms.

A *misalignment* occurs when the relative spatial or temporal separation of two sensorimotor systems changes, or when input to these systems is manipulated to effect an equivalent change. In the present work, the term *visuomotor misalignment* refers specifically to a misalignment between the sensorimotor system comprising the retina and oculomotor muscles and any other sensorimotor system (e.g., the neck or the hand). For example, under both temporal and spatial visuomotor misalignment, a motor command intended to result in an straight ahead hand-pointing movement 200 ms into the future might instead produced visual feedback consistent with a 10 degrees leftward pointing movement 500 ms hence. But the misalignment is between two sensorimotor systems: Initially, at least, the proprioceptors in the arm (and the tactile receptors on the fingers, if the participant can touch the target) should agree with the efferent copy of the motor action in the arm, and the oculomotor proprioceptors and efferent copies should agree with the visual sensory information.

It is important to emphasize the definition of visuomotor misalignment being used here because, although it is common in the literature, it does not follow unambiguously from the form of the word. One might expect visuomotor misalignment to refer to misalignment between visual sensory (retinal) information and visual motor (oculomotor) information; in other words a misalignment within a single sensorimotor system (an *intrasystem misalignment*). Although such intrasystem misalignment can be studied, the bulk of the literature on spatial adaptation (and all of the literature on temporal adaptation) has focused on misalignment between sensorimotor systems (*intersystem misalignment*), and that is the sole focus of the present work too. The term *visuomotor* is retained here for two reasons: It is very commonly used to refer to intersystem adaptation of the sort described here; and it is not wholly inappropriate, for it does concern adaptations to misalignments between motor actions (executed by a non-ocular sensorimotor system) and the visual consequences of them (as apprehended via the visual oculomotor sensorimotor system).

A task involves *visuomotor coordination* if successful performance depends on the use of visual information to select appropriate motor actions. If the relevant visual information includes spatial information (e.g., the location of a resting mosquito), such a task is vulnerable to spatial visuomotor misalignment. If it also includes temporal information (e.g., when a passing mosquito will come within squashing distance), it is vulnerable to temporal visuomotor misalignment as well.

The uncompensated effects of a visuomotor misalignment (whether a temporal delay or a spatial displacement) on performance error in a visuomotor coordination task are the *direct effects*. *Adaptation* refers to all processes that serve to reduce the direct effects. *Perceptual adaptation* is a perceptual learning process that reduces the perceived visuomotor misalignment. Any world learning processes contributing to reduced performance error are referred to as *behavioural adaptation*. *Aftereffects* are changes in behaviour or perception after exposure to a visuomotor misalignment, relative to behaviour or perception before exposure. The core design of the adaptation experiments presented in this thesis is a *pre-test | exposure | post-test* design. In the exposure phase, participants are exposed to misaligned visuomotor feedback. To assess the effect of exposure on perception or behaviour, one or more *criterion tasks* are run, first during the pre-test, and then again during the post-test. The criterion tasks may be visuomotor coordination tasks or perceptual judgment tasks that involve identifying the location (for spatial misalignment) or timing (for temporal misalignment) either absolutely within each of the involved sensorimotor systems or, as in all the experiments in the present work, relatively between the two involved sensorimotor systems.

Adaptation to Visuomotor Misalignment in Space and Time

Adaptation to naturally occurring changes in the spatial relationship among sensorimotor systems is not easily studied. The changes induced by developmental growth are slow to occur, and more sudden pathological changes such as an acquired squint (Watson & Fielder, 1987) are of course not of a magnitude that can be manipulated or determined in advance. Placing prisms in front of a person's eyes has been used to effect an experimentally manipulable alteration in the apparent spatial relationship between the eyes and the rest of the body (Helmholtz, 1867/1962; Held & Freedman, 1963; Redding & Wallace, 1997a). The prisms can be used to produce a lateral displacement of perceived visual space. Typically (see Redding, Rossetti, & Wallace, 2005; or Rock, 1965, for a review), research in this area has used visuomotor coordination tasks, such as reaching towards a point-like visual target (e.g. Helmholtz, 1867/1962; Held & Gottlieb, 1958), or locomotion in a structured environment (e.g. Held & Bossom, 1961).

The prism adaptation paradigm usually consists of three phases, in a form of learning paradigm with an exposure period preceded by a pre-test and followed by a post-test to assess the impact of the learning. The pre-test involves performing a criterion task. The criterion task is designed to provide a measure of the current state of spatial alignment between the eye-head sensorimotor system and the hand-head sensorimotor system, and is performed without any prismatic displacement, usually without sensory feedback or knowledge of results (Redding et al., 2005), to ensure that neither perceptual nor cognitive information is available to alter the state of alignment and motivate readaptation. The second phase is the exposure phase, in which a visuomotor coordination task is performed while wearing the prism goggles, with visual feedback of the results of the action (Redding & Wallace, 1997a), to ensure that the consequences of the distortion are available to the participant. Finally, following the exposure phase, the prism goggles are removed and the criterion task is repeated.

The response to visuomotor spatial misalignment can be detected by various means: initial pointing errors in the direction of the displacement are reduced over a period of exposure to the prisms (adaptation), eventually returning to pre-exposure levels; reaching towards a visual stimulus without feedback is displaced in the direction opposite the prismatic displacement, after the prisms have been removed (a behavioural aftereffect); and perceptual measures of visual and proprioceptive straight-ahead show shifts in the direction of the displacement and opposite the displacement respectively (a perceptual aftereffect). In this section, I discuss these findings in more detail, and consider whether equivalent results have been found in relation to temporal misalignment.

Direct Effects

In a visuomotor coordination task, visuomotor spatial misalignment initially produces performance error, as well as perceptual error. The effect of wearing, for example, base-left prisms is to displace all perceived visual locations to the right, while leaving all other sensorimotor systems unaffected. Thus, if one tried to point at an object, one would aim for a position to the right of its true location, and miss the object by being too rightwards. Similarly, if one introduced a delay between motor and visual time, one would detect a moving object reaching an appropriate interception location too late, thus missing the object by being too late.

With temporal misalignment in continuous motion, one would expect an additional direct effect of the misalignment. As well as performance lagging behind an intended trajectory, one would also expect overshoots. If one attempted to accelerate forward but, because of an uncompensated visuomotor misalignment, saw no consequences of that attempt, one might continue to accelerate, thus overshooting one's intended speed or position. Any subsequent correction would also be subject to the risk of overshoot. Thus, one would expect direct effects in two ways: an increase in the temporal lag of actions behind their intended trajectory, and an increase in variable spatial error around that lagged trajectory.

Smith, McCrary, and Smith (1962) found that delayed visual feedback in a variety of visuomotor tasks had a deleterious effect on performance. However, in contrast to the typical response to spatial misalignment, here they found no evidence of subsequent adaptation. Indeed, on the basis of this and other similar results finding no adaptation to delayed visual feedback, Smith, Wargo, Jones and Smith (1963) concluded that humans are incapable of adapting to changes in visuomotor temporal alignment.

Adaptation

Around the same time that Smith et al.'s (1962) participants were failing to adapt to temporal misalignments, adaptation to visuomotor spatial misalignment, as induced by prisms, was being elicited quite successfully (e.g. Held & Bossom, 1961). For example, a typical exposure task requires participants to point at a visual target (e.g. Helmholtz, 1867/1962). During exposure to spatial misalignment, participants adapt to the prismatic displacement, and their initial performance error gradually reduces and reaches the level of performance found without the prisms (*error reduction*). This adaptation generally occurs within about 15 trials, with performance error reducing to pre-exposure levels (see Redding et al, 2005, for a review).

As noted above, Smith et al. (1962) were unable to identify any adaptation to temporal misalignment. In contrast to Smith et al.'s (1962) findings, Cunningham, Billock, and Tsou (2001) demonstrated successful adaptation to visuomotor temporal misalignment. In a paradigm comparable to that used in prism adaptation experiments involving movement through a structured environment (such as Held & Bossom's, 1961, study), participants' performance at an obstacle avoidance task was measured. In every trial, a computer display showed a cursor falling at a fixed vertical speed through the obstacle field, while participants controlled its horizontal movement with a computer mouse. In a pre-test and a post-test phase, visual feedback was 'immediate' (although in fact, due to the processing speed of the computer used in this study, this meant that there was an imperceptible delay of 35 ms), and different vertical speeds were randomly interleaved. In an exposure phase, visual feedback lagged behind the participants' mouse movements by 235 ms; and the vertical speed gradually increased, depending on participants' success at each successive speed. For participants in a control group, the exposure phase was replaced by an equivalent period of time watching a video. Performance was measured by taking the proportion of trials at a given speed that a participant successfully traversed the obstacle field. Cunningham, Billock, and Tsou (2001) found a pattern of behaviour similar to that found in prism adaptation. Performance at the start of training was poor relative to that in the pre-test (direct effects), and improved over the course of training (adaptation).

Cunningham, Billock, and Tsou (2001) explained the difference between Smith et al.'s (1963) findings and their own by arguing that, whereas in previous temporal adaptation research participants were able to slow their behaviour down so as to be less affected by the visuomotor misalignment, the fixed vertical speed in each trial of their experiment prevented this. The spatial error consequent on a given temporal delay is smaller, the smaller the velocity of the object. By constraining participants to a fixed velocity so that they were exposed to the consequences of the delay, Cunningham, Billock, and Tsou (2001) reasoned, adaptation was enabled, and it occurred fairly swiftly, over about three minutes.

Miall and Jackson (2006) have also shown reduction in behavioural error over the course of exposure to visuomotor temporal misalignment. In Miall and Jackson's task, in which a relatively unpredictable visual target was tracked with a joystick, adaptive performance appeared to take longer to develop, showing no improvement during the first day (an exposure duration of one hour). Perhaps the predictability of the regular, non-randomized obstacles in Cunningham, Billock, and Tsou (2001) was another aspect of the procedure that enabled rapid adaptation comparable to that found in adaptation to visuomotor spatial misalignment. If a participant had no reliable prediction (whether for behavioural or perceptual use) of obstacle or target locations over the timescale of the delay, any compensation for the delay would also be unreliable. Without accurate prediction over the required timescale, one could not produce motor actions that would track the visual location of an object despite delays in the production of the motor action and in the acquisition of visual information. An analogy in the spatial domain would be arise if a participant's vision were rotated so far to the right that the region of space accessible to her right arm (motor space) had no overlap with the region of space visible to her eyes (visual space). The participant would never be able to point (with her right arm) at any visible visual target.

The predictability and the size of the misalignment may combine, then, to prevent effective adaptation. If a moving object were perfectly predictable, one could interact accurately with it, no matter how large a visuomotor misalignment. Likewise, if one had zero visuomotor misalignment (i.e. instantaneous transmission between visual information being acquired and subsequent motor actions), one could interact with any moving object, however unpredictable it was: on sensing its current position, one could instantaneously move an effector to that position and interact with it. Miall and Jackson's (2006) task is more relevant to natural behaviour than one with completely predictable task characteristics: Many interesting things in the world that one might want to interact with or avoid (for example, prey or predators) are less than perfectly predictable. However, movement in the world is continuous and is thus, in principle, approximately predictable over sufficiently short timescales.

Furthermore, behaviour is typically not wholly random: For example, cockroaches respond to threatening stimuli by choosing unpredictable initial headings that are, nonetheless, predictably roughly in a direction away from the threat (Domenici, Booth, Blagburn, & Bacon, 2008). Thus, although excessive unpredictability may preclude adaptation, approximate and incomplete predictability may be both natural and amenable to adaptation.

Aftereffects

With visuomotor coordination tasks, then, visuomotor spatial misalignment is compensated for. And, in certain circumstances, perhaps contingent on the predictability of the task and the size of the misalignment, visuomotor temporal misalignment is also compensated for. In spatial misalignment, an aftereffect follows removal of the misalignment, exhibited both in behaviour and in visual and proprioceptive perception. Behavioural aftereffects are found in the direction opposite the prismatic displacement. In other words, after exposure to, say, a base-left prism - which displaces the visual field rightward - performance error is to the left, relative to performance in the pre-test (Redding et al, 2005). Such performance aftereffects may arise partly from transfer of world learning of the appropriate behavioural response (e.g. Welch, Choe, & Heinrich, 1974). If the criterion task is an active task similar to the exposure task, co-ordinative strategies that were effective during exposure might continue to be used during the post-test. However, if this were the only source of aftereffects, one would not expect to detect aftereffects using purely perceptual measures in each of the involved systems. But studies (e.g. Redding & Wallace, 1994) that have measured aftereffects by asking participants to adjust a visually perceived dot until it appears straight ahead, or by asking them to position their arm so that it feels straight ahead have found perceptual aftereffects of adaptation.

Thus, in the case of spatial misalignment, both perceptual and world learning are involved, and may be distinguished experimentally. Adaptive behaviour reaches 100% compensation quickly, but perceptual aftereffects develop more slowly, and – when not contaminated by transfer of motor learning - reflect only 40% of the prismatic displacement (Redding et al., 2005), even after multiple days of exposure (Hay & Pick, 1966). The dissociability of perceptual aftereffects from the behavioural components of adaptation is further evinced by Pisella et al.'s (2004) report that a patient with lesioned posterior parietal cortex showed slower development of adaptive behaviour compared with normals, while producing similar aftereffects, whereas Weiner, Hallett, and Funkenstein, (1983) found adaptive behaviour but no aftereffects in patients with cerebellar lesions. Redding et al. (2005) argue that this provides further evidence for the existence of at least these two routes to adaptation in the case of spatial misalignment.

In the case of visuomotor temporal misalignment, though, it is as yet unclear whether both world and perceptual learning are involved. However, there is evidence of adaptive behaviour, and Cunningham, Billock and Tsou (2001) also demonstrated behavioural aftereffects of the adaptation. In the post-test of their study, participants performed 10 trials with immediate visual feedback, with a vertical speed identical to the highest vertical speed at which they, in the pre-test, met a success criterion of avoiding crashing on at least eight out of 10 trials. Participants who had been exposed to visuomotor misalignment crashed more often in the post-test than in the pre-test, and more often than control participants who had watched a short film instead of exposure. Miall and Jackson (2006) found a behavioural aftereffect (assessed by measuring spatial error during 'catch trials', in which the delay was removed half-way through the trial) early in the first day of training, and no change in its size over the five days of training. However, neither Cunningham, Billock, and Tsou (2001) nor Miall and Jackson (2006) used perceptual criterion tasks, and so the contribution (if any) of perceptual learning to the error reduction or behavioural aftereffects is unclear.

In a study of responses to intersensory (auditory-visual) temporal misalignment, Fujisaki, Shimojo, Kashino, and Nishida (2004) found perceptual aftereffects of exposure to auditory-visual temporal misalignment. They assessed perceptual change using simultaneity judgments and the stream-bounce effect, an illusion in which relative auditory/visual timing effects whether two circles appear to stream through or bounce off each other (Julesz, 1995). They found a small but significant effect of exposure on relative perceptual timing of auditory and visual stimuli, both explicitly in the judgment criterion task and implicitly in the stream-bounce criterion task. However, this study was concerned with adaptation to intersensory misalignment. It remains possible that the problem of temporal misalignment is solved behaviourally when the exposure task entails visuomotor coordination, but is solved through perceptual learning in the case of inter-sensory misalignments.

A perceptual aftereffect of exposure to delayed feedback in a visuomotor judgment task has been demonstrated by Stetson, Cui, Montague, and Eagleman (2006). They found a shift in the point of subjective simultaneity between button presses and visual flashes in a temporal order judgment task, when exposed to brief delays between button presses and causally related flashes. They found significant effects of exposure to 100 ms delays, but not any at 250, 500, and 1000 ms delays, with smaller effects the larger the exposed delay. However, despite the use of motor actions (button presses) in their exposure task, there was no visuomotor coordination task in this experiment: Visual information was not needed to inform the timing of motor actions. Thus, as with Fujisaki et al.'s (2004) intersensory exposure phase, there was no behavioural learning to be done.

Adaptation and both behavioural and perceptual aftereffects have been demonstrated in temporal misalignment. However, the paradigms with which perceptual aftereffects (and not behavioural aftereffects) have been demonstrated differ markedly from those with which behavioural aftereffects (and not perceptual aftereffects) have been found. It is, therefore, impossible to draw conclusions about the nature of visuomotor temporal adaptation from this body of research.

Distinguishing Perceptual and Behavioural Adaptation

Behavioural Measures Cannot Directly Assess Perceptual Adaptation

What options, then, are available for distinguishing perceptual and behavioural adaptation to visuomotor temporal misalignment? In a predictable task, any error reduction could be explained equally by perceptual or behavioural adaptation: Performance error would transparently be removed as a consequence of removing the perceptual discrepancy. For example, consider a task in which a participant is asked to synchronize a repeated motor action with a predictably periodic visual stimulus, and in which visual feedback of the motor actions was delayed. If the delay were compensated for by perceiving visual events as occurring commensurately earlier, motor actions would then be timed relative to the adjusted visual timing (veridically) rather than the delayed visual timing. But performance error may be removed without altering perception at all. Assuming that, as in Cunningham, Billock and Tsou's (2001) task, any obstacles or targets can be predicted in advance, a participant may compensate for the delay added to the relationship between hand movements and visual feedback of them by altering the timing of motor actions for a given stimulus event (such as an approaching obstacle or target), rather than by altering the perceived timing of the stimulus events or of the motor actions. Thus, participants could make their hand movements earlier than would otherwise have been necessary to avoid the obstacles. Performance error would be removed because the participant would have learnt how successfully to avoid obstacles in the task, despite perception remaining unchanged.

Following Cunningham, Billock, and Tsou's (2001) work, Cunningham, Chatziastros, von der Heyde & Bülthoff (2001) attempted to find evidence of perceptual adaptation in visuomotor temporal adaptation, again using only behavioural measures. Using a driving simulator, they investigated adaptation to visuomotor temporal misalignment and generalization to streets with different shapes from those used during exposure. As in Cunningham, Billock, and Tsou (2001), there was no quantitative measure of behavioural temporal aftereffect, but measures of number of streets completed and number of steering wheel reversals showed aftereffects of adaptation. Furthermore, when tested on a mixture of novel and already seen streets, there was no difference on the street completion measure between the old and new streets.

Cunningham, Chatziastros, et al. (2001) argued that this complete generalization indicated that perceptual adaptation had taken place, since world learning typically transfers less to novel tasks than to already-trained tasks. However, the same region of visual space was involved in both the novel and the old streets and, crucially, the same strategies – such as turning early for each bend – would be successful. Cunningham, Chatziastros, et al. (2001) drew attention to research which suggests that humans may be unable consciously to make sufficiently precise predictions to enable a successful early turning strategy (e.g. Wagenaar & Sagaria, 1975). However, Wagenaar and Sagaria's (1975) study found considerable underestimation of exponential growth, and did not investigate predictions of linear growth. Since the speed of the car was constant for every trial, like in Cunningham, Billock, and Tsou's (2001) obstacle avoidance task, the participants in Cunningham, Chatziastros, et al.'s (2001) study would have needed to make precise judgments of linear growth, if anything, not exponential growth. In fact, all that would have been required would be to make an appropriate turning at a fixed distance prior to each bend.

Measures of performance cannot directly distinguish between perceptual and world learning. The most obvious solution, then, would be to use perceptual criterion tasks. Perceptual adaptation, in which the perceived timing of stimuli is altered in either of the involved sensorimotor systems, should be detectable in criterion tasks such as temporal order judgments (as used by Stetson et al., 2006) or time-related illusions such as the stream-bounce effect (as used by Fujisaki et al., 2004). Conversely, world learning of a new set of responses for given task-related percepts should not be detectable through such measures: Perception has not been altered, so any perceptual measures should be identical before and after adaptation. Perceptual measures of adaptation are a mainstay of the visuomotor spatial misalignment research, and I use temporal order judgments in a manner akin to Stetson et al.'s (2006) in each experiment from Experiment 2.2 onwards. However, it is possible that performance measures may more indirectly distinguish perceptual and world learning components of adaptation. In Experiments 2.0 and 2.1, I used the persistence of perceptual adaptation relative to world learning as an alternative route to identifying a perceptual component to visuomotor temporal adaptation. In what follows, I justify this choice by presenting a theoretical argument in favour of the claim that perceptual adaptation, and not behavioural adaptation, should survive performance of a visuomotor coordination task without visual feedback of the motor actions, unless the adaptation spontaneously decays. I then argue that the literature on visuomotor spatial misalignment suggests that, whereas behavioural adaptation spontaneously decays, perceptual adaptation does not. Thus, with the appropriate task, aftereffects should persist if they are perceptual in nature, and wane if they are not.

Behavioural Measures Can Provide Indirect Evidence for Perceptual Adaptation

Whatever is learnt during adaptation, whether it be perceptual learning or world learning, it may be unlearnt through two routes: a rejection of the adapted learning in favour of pre-existing learning as the information that motivated the adapted learning becomes more distant in time (*decay*); or a rejection of the adapted learning in favour of new, contradictory information (*readaptation*). By this definition of decay, only the passing of time is needed. For readaptation, as for adaptation, two categories of error may be available: performance error (which could motivate behavioural readaptation), and visuomotor misalignment (which could motivate perceptual readaptation). Participants may detect performance error by comparing their motor actions (whether efference copies of their motor actions or the proprioceptive or visual feedback of their motor actions) with relevant visual targets or obstacles. Visuomotor misalignment could be detected wherever there are representations of a motor action in multiple modalities (efference copies, proprioceptive feedback, visual feedback), and those representations conflict with each other. These sources of information (performance error and visuomotor misalignment) are each available during the performance of some sorts of tasks but not others, and in the presence of either perceptual or behavioural adaptation. If there exists a type of task that would, in the presence of now-irrelevant behavioural adaptation, provide a participant with performance error, but which would, in the presence of now-irrelevant perceptual adaptation, provide neither performance error nor visuomotor misalignment; then such a task would produce readaptation in the case of behavioural learning, and no readaptation in the case of perceptual learning.

If participants were performing no task at all, or if they were performing a purely perceptual task that required no active movement, there could be no source of either type of error: Visuomotor misalignments and performance error cannot be detected in the absence of motor actions. Thus, in this case, the only route to the pre-adaptation state would be decay. If participants were performing an active open-loop task (i.e., if they had no visual feedback of their motor actions), performance error could be detected by comparison of information from the efference copy of the motor command (or associated proprioceptor feedback) and the visual targets or obstacles. However, because the participants would have no visual feedback of their motor actions, there could be no detection of visuomotor misalignment. If participants were instead performing an active closed-loop task (i.e., if they had visual feedback of their motor actions), they would still be able to detect performance error, but would additionally be able to monitor discrepancies between the expected trajectory of their hand movements (whether through efference copies or proprioception) and visual feedback of the same hand movements.

Thus, in the absence of spontaneous decay, inactivity should produce no readaptation, an open-loop task may produce behavioural readaptation, where performance error is available, and a closed-loop task may additionally produce perceptual readaptation, if visuomotor misalignment is present. In the case of spatial displacement, for example, a participant may adapt to prisms that shift visual space rightwards by representing visual space leftwards. The behavioural consequence after removal of the prisms would be to perceive a straight ahead visual target as being off to the left, and to point leftwards accordingly. If the task were closed-loop, the participant would then unexpectedly see their hand off to the left of the target: performance error, and a visuomotor misalignment between the expected and observed motor action. If it were open-loop, however, the participant would see the target to the left and perceive that they had made a motor action equally to the left; there would be no visual feedback of their action to contradict this percept.

The non-persistence of aftereffects has been noted in adaptation to visuomotor spatial misalignment (e.g. Choe & Welch, 1974; Fernandez-Ruiz, Diaz, Aguilar, & Hall-Haro, 2004). Choe and Welch (1974) found decay in aftereffects in a repeated measures design over the course of 15 minutes. In this experiment, the criterion tasks comprised a visuomotor coordination task, and both a proprioceptive and a visual task. The visuomotor task (active pointing to a visual target, without visual feedback of the pointing action) would, in post-test, have provided an opportunity for detecting normal visuomotor alignment in the post-test, which could have motivated perceptual readaptation in the hand-head proprioceptive-motor system but not the eye-head visual system. Indeed, Choe and Welch (1974) found decay in the visuomotor and proprioceptive tasks but not the visual task.

With a between-subjects design and a (similar to exposure, visuomotor) criterion task, Fernandez-Ruiz et al. (2004) found a decay of 40% over 10 minutes, leaving the aftereffect still significantly different from zero, followed by no change in aftereffect for the following 10 minutes. The use of a between-subjects design ruled out readaptation due to normal visuomotor alignment, because participants were not repeatedly exposed to normal visuomotor alignment at varying times after the end of exposure; but rather, separate groups of participants each had varying periods of complete inactivity before being tested. This partial decay followed by a plateau suggests that, in adaptation to spatial misalignment, when testing confounds perceptual and behavioural adaptation, an initially present behavioural component decays. Combined with Choe and Welch's (1974) findings, it appears that (unless the relevant system is exposed to normal visuomotor alignment) a perceptual component persists. Thus, the persistence of aftereffects in an open-loop visuomotor task may serve as an indirect indication of perceptual adaptation.

Overview of Thesis

In Chapter 1, I present a direct replication of Cunningham, Billock, and Tsou's (2001) ground-breaking study of visuomotor temporal adaptation. I found that the main finding of a behavioural aftereffect did not replicate in this study, although correlational analyses suggested that a weak behavioural aftereffect may have been present in some participants. I identify two major differences between Cunningham Billock, and Tsou's procedure and typical methods used in the literature on spatial adaptation. In Cunningham Billock, and Tsou's study, behavioural (not perceptual) aftereffects measures were used, and objectively normal visual feedback of motor actions was available in the post-test phase. The former difference could tend to promote behavioural aftereffects in the absence of perceptual adaptation; the latter could tend to suppress aftereffects from any source.

Thus, I developed a new method that would allow the criterion task to be performed with or without visual feedback of motor actions, to avoid suppression of aftereffects in the post-test phase. With this method, I found a persistent behavioural aftereffect, which, I argue, is more consistent with perceptual adaptation than with behavioural adaptation alone. This study is presented in Chapter 2. Also in Chapter 2, purely perceptual measures of visuomotor alignment were added, to confirm whether the aftereffects found were perceptual in nature. Here I found no evidence of perceptual aftereffects;

thus it appears that, in this task, a purely behavioural solution to the misalignment had been adopted.

Perhaps, then, the task was too simple: a very straightforward adjustment of the phase of participants' movements (equivalent to a strategy of side-pointing in spatial adaptation) would have been sufficient to solve the problem of the sensory-motor delay. Furthermore, participants were exposed only to a limited range of velocities and accelerations (since the task involved only simple sinusoidal movement). Thus, in Chapter 3, I used a richer visuomotor coordination task, with less predictable targets. The argument I advance concludes that exposure to visuomotor temporal misalignment in visuomotor coordination tasks does not result in a perceptual change measurable in judgment-based perceptual criterion tasks, but may be investigated indirectly using simulation models of behavioural performance.

Chapter 1: Cunningham, Billock, and Tsou (2001) does not replicate

It has been suggested that human sensorimotor systems may maintain effective mutual alignment for perception and action in the face of changes to the temporal relationships among them in much the same way as they do for changes to the spatial relationships among them. Cunningham, Billock, and Tsou (2001) have demonstrated that humans can adapt to, and show behavioural aftereffects of, temporal visuomotor adaptation under appropriate conditions. In the present study, Cunningham, Billock and Tsou's (2001) finding of a behavioural aftereffect of exposure to a temporal misalignment did not replicate; but a correlational analysis suggested that, for some participants at least, a small aftereffect was present. I discuss features of the procedure that may have inhibited reliable detection of aftereffects, and note problems with interpreting any aftereffect obtained using Cunningham, Billock, and Tsou's (2001) procedure.

As outlined in Chapter 0, Cunningham, Billock, and Tsou (2001) provided the first indication that, under the right circumstances, behavioural adaptation can be observed to temporal visuomotor misalignment. Their participants performed a visuomotor obstacle avoidance task, controlling the horizontal motion of a cursor that fell through an obstacle course at a fixed vertical speed, with or without a delay between their actions and their effects on the cursor. They noted that, whereas in previous temporal adaptation research participants were able to slow their behaviour down so as to be less affected by the temporal visuomotor misalignment, the fixed vertical speed in each trial of their task prevented this. By forcing participants to be exposed to the consequences of the delay, Cunningham, Billock, and Tsou (2001) reasoned, adaptation was enabled. However, another factor may have enhanced the detected behavioural aftereffect detected after exposure to visuomotor misalignment in this task: the vertical speed at which the post-test was conducted.

In Cunningham, Billock, and Tsou's (2001) study, the vertical speed of an 'aeroplane' icon (a white square) in the post-test was determined by the speed at which each participant achieved a success criterion in the pre-test. Cunningham, Billock, and Tsou (2001) reported the speeds, but did not present an analysis of them. My analysis of the raw data they reported (see Table 1 of Cunningham, Billock, & Tsou, 2001, for the raw data) shows that the mean speed in the experimental condition was higher (6.0 cm/s, *SE* = 0.5) than in the control condition (4.7 cm/s, *SE* = 0.4), and a two-tailed t-test showed that the difference was marginally non-significant, $t(18) = -2.09$, $p = .05$, $\eta_p^2 = .20$. Thus, the speed at which participants performed the post-test tended to be confounded with exposure condition, and this may in part explain the strength of the effect they detected.

It is possible that higher speeds in the experimental condition's post-test could account for greater performance error in that post-test. However, since the pre-test trials with which the post-test trials were being compared were always the ones performed at the same speed as in post-test, a direct effect of speed on performance error could not explain the greater aftereffects. Any impact on post-test would be equal to that on pre-test. However, higher post-test speeds would amplify the spatial consequences of any actual temporal aftereffects. For any given size of aftereffect, the temporal error would translate into larger distances on the screen for faster speeds. Thus, for a fixed temporal aftereffect (regardless of whether it is perceptual or behavioural in nature), faster speeds should lead to more crashes, and thus a larger measured aftereffect. As this would predict, a one-tailed Pearson's correlation test showed that there was a significant moderate negative correlation between speed and measured aftereffect (post-test success rate, minus pre-test success rate, divided by pre-test success rate), within the experimental condition, $r(8) = -.71$, $p = .01$, while in the control condition there was no relationship, $r(8) = .01$, $p = .51$.

To assess whether the strength of Cunningham, Billock, and Tsou's (2001) aftereffects could in part be explained by this confound between exposure condition and test speed, I conducted an ANOVA of aftereffect in terms of condition and speed on their data (see Table 1 of Cunningham, Billock, & Tsou, 2001). The resulting model was a good fit (adjusted $R^2 = .74$), and was significant, $F(3,16) = 19.14$, $p < .01$, $\eta_p^2 = .78$. The interaction between condition and speed was marginally non-significant, $F(1,16) = 3.72$, $p=0.07$, $\eta_p^2 = .19$. A model with the interaction term removed was a good fit (adjusted $R^2 = .70$), and was significant, $F(2,17) = 19$, $p < 0.01$, $\eta_p^2 = .73$. The main effect of speed was marginally non-significant, $F(1,17) = 3.62$, $p = .07$, $\eta_p^2 = .18$, and the main effect of condition was significant, $F(1,17) = 25.16$, $p < .01$, $\eta_p^2 = .60$. Thus, this analysis does not undermine Cunningham, Billock, and Tsou's (2001) claim that an aftereffect of adaptation was detected even though, after the impact of speed on aftereffects in the delay condition was taken into account, the size of the effect was somewhat reduced.

In this chapter, I present a replication of Cunningham, Billock, and Tsou's

(2001) experiment, conducted with a view to extending it in future studies, if it replicated successfully, to investigate the nature of the adaptive learning and aftereffect. As in Cunningham, Billock, and Tsou's (2001) experiment, of which what follows is an exact replication, the expectation was that participants in the delay condition would have a greater pre-post decrease in success rate than those in the control condition.

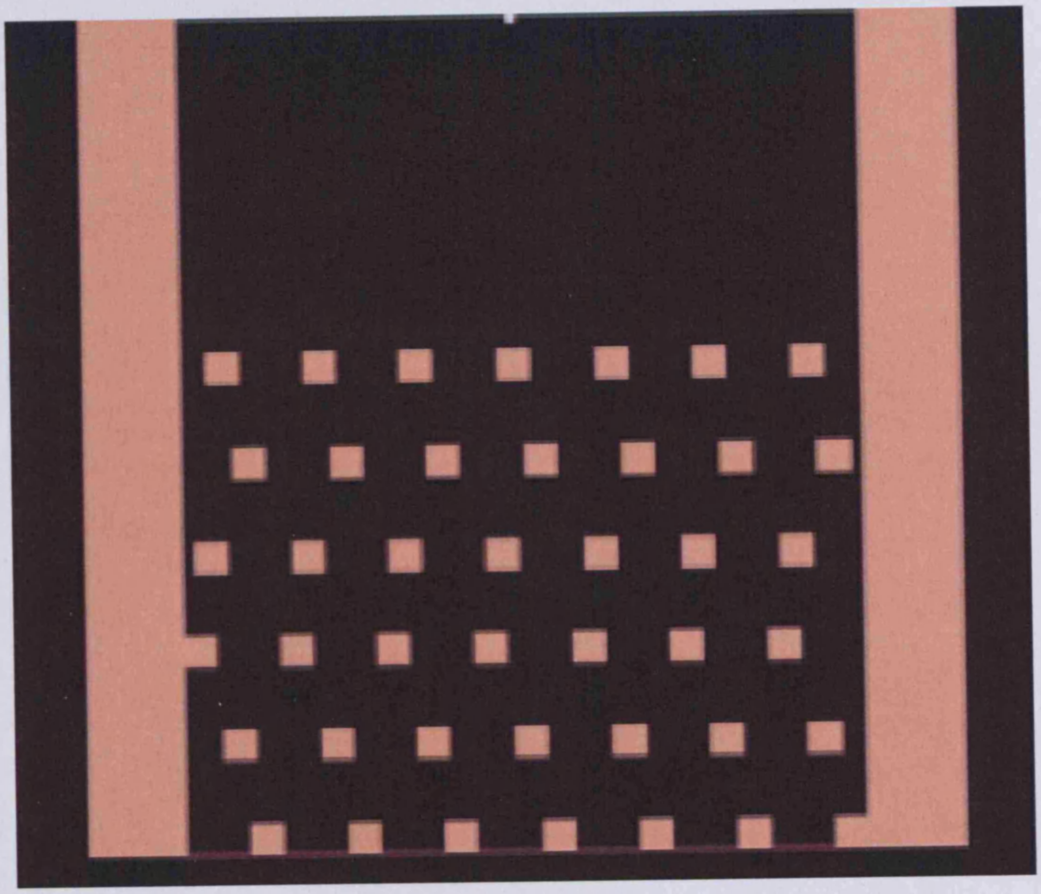

Figure 1.0. The display used in Experiment 1.0. Participants controlled the horizontal motion of the 'aeroplane' (the white square centred at the top of the screen) as it fell at a constant vertical speed. The task was to avoid crashing into the obstacles or the walls.

Method

Participants

Twenty participants, the same number as were used by Cunningham, Billock, and Tsou (2001), were recruited from the undergraduate participant panel at Cardiff University. The participants were randomly assigned to each of the two conditions.

Displays

The display was produced using the Delphi programming language and OpenGL library on a computer running Windows XP. Participants were seated at approximately 50 cm from a 1024x768 pixel computer screen with a refresh rate of 60 Hz. Their task in each trial was to manoeuvre a small (0.2 cm) white square (the 'aeroplane') through an obstacle field. The obstacle field consisted of 6 rows and 7 columns of square (0.7 cm) obstacles, flanked by 'walls' to the left and right. The obstacles were arranged such that there was no straight vertical path through the field and such that each row was separated by 1.4 cm from the nearest rows, and each obstacle was separated by 1.4 cm from each of the neighbouring obstacles within its row. The same arrangement of obstacles was used throughout all trials (see Figure 1.0, for a picture of the display).

The aeroplane travelled at one of ten fixed vertical speeds (2.9, 3.2, 3.5, 3.9, 4.4, 5.0, 5.9, 7.1, 8.8, and 11.8 cm/s) from the top of the screen to the bottom. The aeroplane's horizontal motion was controlled by participants by using a computer mouse, which was isometric (i.e. the horizontal movements of the aeroplane were identical in size to those of the mouse).

Procedure

There were two conditions (delay | control), varied between participants. There were three consecutive phases (pre-test | training | post-test) within the experiment, each of which consisted of a number of trials, specified below. In each trial, participants attempted to manoeuvre the aeroplane through the obstacle field. The trial terminated as soon as the aeroplane crashed into any obstacle or wall, or successfully traversed the field. Following completion of each trial, a red cross (indicating a crash) or a blue tick (indicating success) was displayed to give participants clear feedback on their performance. During the pre-test and post-test phases, there was no lag between mouse movements and visual feedback, beyond any delay inherent in the hardware (c. 16 ms). Prior to each trial in these phases, the aeroplane's speed was demonstrated by showing it falling through the lowest third of the screen. In the delay condition, during the training phase, visual feedback lagged behind the mouse movements by an additional 200 ms, which was found by Cunningham, Billock and Tsou (2001) to be a delay sufficient to cause a deterioration in participants' performance.

During the pre-test, each of the ten speeds was presented five times, in random order, with each speed being presented once before any speed was presented again. The fastest speed at which a participant managed to traverse the field on at least four of the five repetitions was recorded as his or her top speed. During the training phase, for participants in the delay condition, the speeds were presented from slowest to fastest. Progression to the next speed was dependent on the participant succeeding on 8 out of 10 consecutive trials. The training phase ended if a participant crashed 10 times consecutively. After 70 training trials, the training phase ended as soon as a participant failed to meet the criterion of succeeding on 8 out of 10 consecutive trials, or after completing 10 trials at the highest possible speed. Participants in the control condition spent an equivalent length of time watching a video, as in Cunningham, Billock, and Tsou's (2001) procedure. D. W. Cunningham (personal communication, December 12, 2005) used this control procedure in the training phase to ensure that participants in both conditions spent the same interval of time engaged in a visual task, and that participants in both conditions had no opportunity to practice the zero-lag pre- and post- test task during the training phase. The post-test phase consisted of 10 trials at the participant's top speed from the pre-test.

For each participant, the success rate at the top speed during the pre-test was recorded, as was the success rate at the same speed during the post-test. The measure of behavioural adaptation was the post-test success rate minus the pre-test success rate, as a proportion of the pre-test success rate More negative values indicated a stronger behavioural aftereffect.

To assess the relative contributions of condition and speed to any aftereffect, an analysis of variance (ANOVA) was conducted, with dependent variable aftereffect, and with independent variables condition and speed. Speed was included in the model because, as argued earlier in this chapter, a given size of aftereffect (as a time interval) would produce larger errors (as a spatial distance) on the screen at a higher speed, and thus be more likely to result in a crash at high speeds than at low speeds.

Results

The mean aftereffect (post-test success rate minus pre-test success rate, divided by pre-test success rate) in the delay condition was -0.078 (*SE* = 0.070), and in the control condition was -0.010 (*SE* = 0.083). A one-tailed *t*-test showed that the difference was not significant, $t(18) = 0.8$, $p = 0.2$.

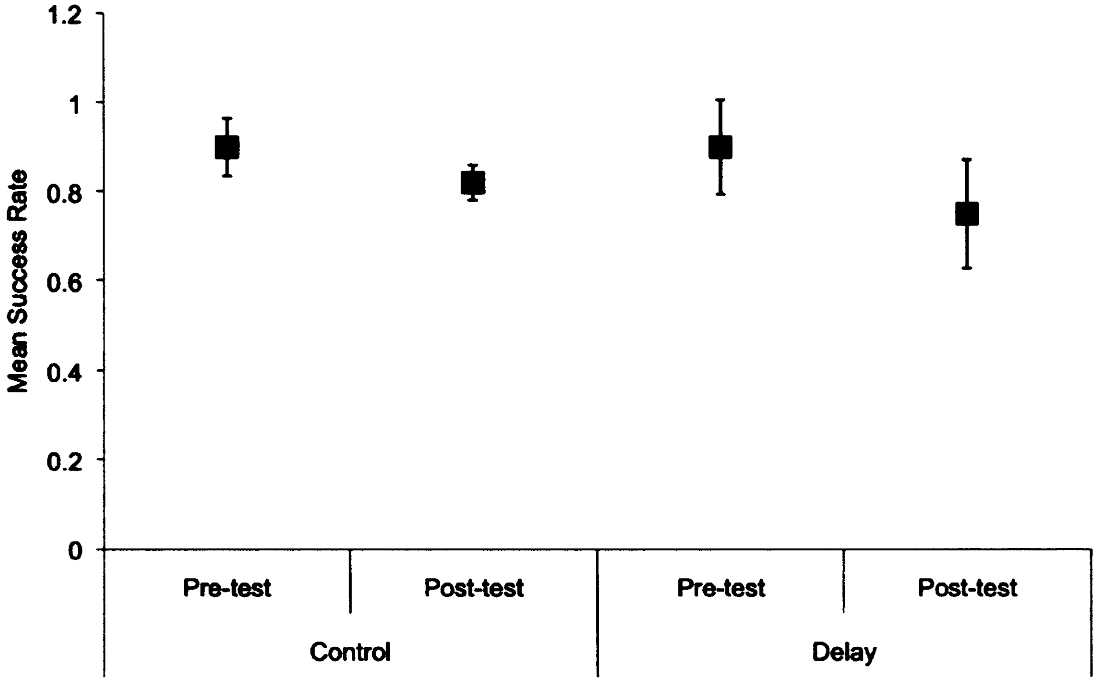

Figure 1.1. Success rate in each condition and phase of Experiment 1.0. A rate of 1 indicates no crashes, and a rate of 0 indicates that every trial was a crash. Thus, adaptation would be evinced by an aftereffect of lower success rates in the post-test. Error bars are 95% confidence intervals.

An ANOVA of aftereffect in terms of condition and speed was not a good fit, with an adjusted R^2 of .07, and not significant, $F(3, 16) = 1.48$, $p = .26$, $\eta_p^2 = .22$. There was no significant interaction between condition and speed, $F(1, 16) = 1.83$, $p = .18$, $\eta_p^2 = .11$. A model without the interaction had an adjusted R^2 of .02, and was also not significant, $F(2, 17) = 1.2$, $p = .33$, $\eta_p^2 = .12$: there were no significant main effects of condition, $F(1, 17) = 0.68$, $p = .42$, $\eta_p^2 = .04$, or speed,

$F(1, 17) = 1.7, p = .21, \eta_p^2 = .09$. Thus, although there was a small behavioural aftereffect in the same direction as in Cunningham, Billock and Tsou's (2001) study, it did not reach significance.

Comparison of Experiment 1.0 and Cunningham, Billock, and Tsou (2001)

As argued earlier in this chapter, the test speed should have equivalent impact on pre-test and post-test performance if there is no aftereffect in the post-test, but should amplify the spatial consequences of any given temporal aftereffect when one is present. My earlier analysis of the raw data reported in Cunningham, Billock and Tsou's (2001) study showed that, in the control condition, speed had no impact on aftereffects whereas, in the delay condition, there was the predicted relationship between speed and aftereffects. Thus, to compare the results of Cunningham, Billock, and Tsou 's (2001) study and the present replication, the data from the present study were combined with the raw data reported by Cunningham, Billock, and Tsou (2001) and a three-way ANOVA was conducted on aftereffect in terms of condition, experiment and test speed. With all interactions included the model was a good fit (adjusted $R^2 = .62$) and significant, $F(7,32) = 10.02, p < .01, \eta_p^2 = .69$. The three-way interaction was non-significant, $F(1,32) < 1, p = .72, \eta_p^2 < .01$. A model without the three-way interaction (adjusted $R^2 = .63$) was significant, $F(6,33) = 11.98, p < .01, \eta_p^2 = .69$, but the experiment x speed interaction was non-significant, $F(1,33) < 1, p = .64$, $\eta_p^2 < .01$. A final model, with the non-significant experiment x speed interaction removed, (adjusted $R^2 = .64$) was significant, $F(5,34) = 15, p < .01$); here, there was a condition x speed interaction, $F(1,34) = 5.33, p = .03$) and a condition x experiment interaction, $F(1,34) = 10.97, p < .01$.

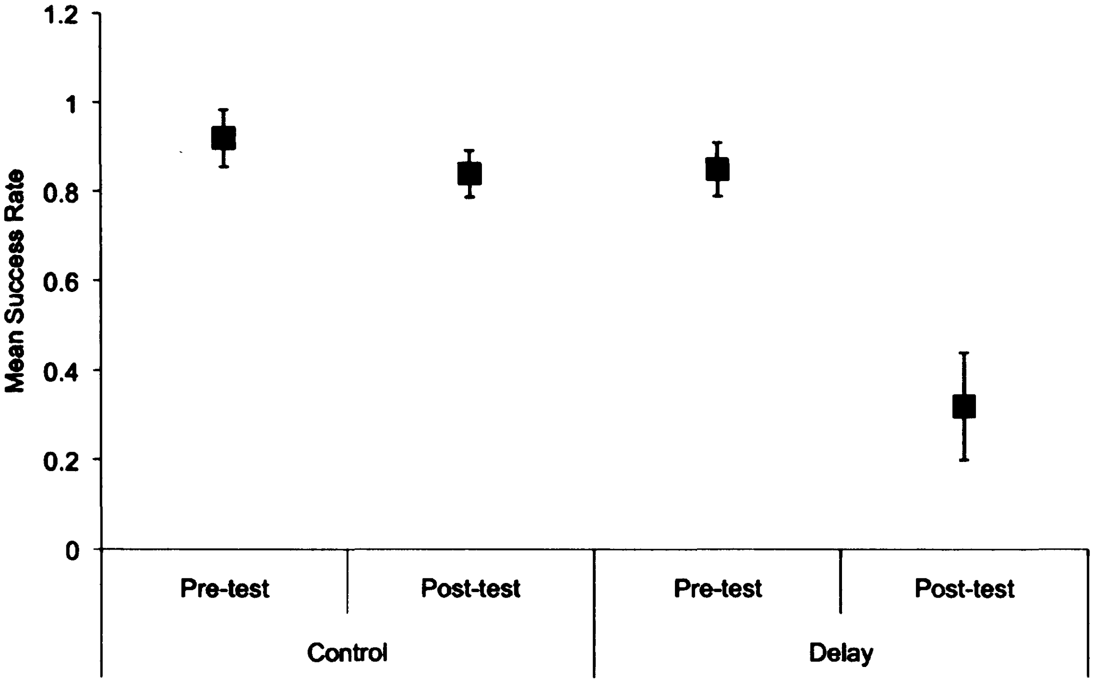

Figure 1.2. Success rate in each condition and phase of Cunningham, Billock, and Tsou's (2001) study (taken from the raw data presented in Table 1 of Cunningham, Billock, & Tsou, 2001). A rate of 1 indicates no crashes, and a rate of 0 indicates that every trial was a crash. Thus, adaptation would be evinced by an aftereffect of lower success rates in the post-test. Error bars are 95% confidence intervals.

That there was a condition by experiment interaction indicated that, in the present study, the effect of condition on aftereffect was reduced. The condition x speed interaction showed, as noted above, that higher speeds amplified the effects of condition. Finally, the absence of any three-way condition x experiment x speed or two-way experiment x speed interaction suggests that the effect of speed on aftereffect was equivalent across the two experiments.

A one-tailed Pearson's correlation test showed that, in the experimental condition of Experiment 1.0, there was a significant moderate negative correlation between speed and aftereffect ($r(10) = -.57, p = .04$), while in the control condition there was no such relationship ($r(10) = .04, p = .54$). This followed a similar pattern to the results for Cunningham, Billock, and Tsou's (2001) data presented earlier in the present chapter.

Discussion

In a replication of Cunningham, Billock, and Tsou's (2001) temporal visuomotor coordination experiment, I found no direct evidence for an aftereffect of adaptation to temporal misalignment. However, the results showed a pattern strikingly similar to one also found in Cunningham, Billock, and Tsou's results: Participants in the delayed feedback condition showed a correlation between test speed and size of adaptive aftereffect. This provides some limited support for the assertion that there was an aftereffect in Experiment 1.0. If there were no real aftereffect (i.e. if errors were distributed similarly in the pre-test and post-test), the measured aftereffect should not be affected by speed. Since they were correlated in the experimental condition, but not in the control condition, this suggests that there may have been an aftereffect in the experimental condition, even though it was too small to be detected as significant by the ANOVA.

The categorical, binary measurements in this study (the success rate measure) made it a rather crude instrument for detecting an aftereffect. For example, if a participant usually turned at or after the mid-point of the 1.4 cm vertical gaps between obstacles, and the aeroplane was moving at a vertical speed of 5.9 cm/s, a real aftereffect of less than (0.7 / 5.9 =) 0.1 seconds would have no effect on the success rate. Since the prism adaptation literature (e.g. Redding et al., 2005), and the intersensory temporal adaptation literature (e.g. Fujisaki et al.'s, 2004), lead one to expect aftereffects of around 40% of the exposed misalignment, one would anticipate aftereffects of around 0.08 seconds, small enough not to impact on performance at all in this scenario.

Furthermore, the availability of visual feedback in the post-test could have caused any aftereffect to be suppressed, as veridical visuomotor alignment returned. This is in contrast to the typical post-test procedure in the literature on spatial adaptation, in which pointing movements are made without visual feedback to assess aftereffects. However, with the sort of obstacle avoidance task used in the present study, the removal of visual feedback would make the task too difficult, as it would require considerably more precise visuomotor coordination than does the normal version of the task. Thus, a task more suited to action without feedback is needed, to effectively detect an aftereffect without suppressing it. Finally, even if Cunningham, Billock, and Tsou's (2001) results had fully replicated in the present study, this would not have been evidence of perceptual adaptation of the sort familiar from the prism adaptation literature.

In this chapter, I reported a failure to replicate Cunningham, Billock, and Tsou's (2001) main finding, but showed that a correlational analysis of the impact of test speed on aftereffects suggested a small aftereffect of adaptation was nonetheless present in this study. I identified several key features of the procedure that may, with this procedure, prevent effective and reliable detection of aftereffects, and make it difficult to distinguish perceptual and behavioural learning. In Chapter 2, I address these concerns, to develop a visuomotor coordination more suited to the study of perceptual and behavioural temporal adaptation.

Chapter 2: A New Paradigm Produces a Behavioural Aftereffect

Sensorimotor alignment varies over the course of development and under different environmental conditions. Previous research has shown that humans can compensate for the resulting temporal misalignment while performing visuomotor coordination tasks (e.g. Cunningham, Billock, & Tsou, 2001), but remains silent on the question of whether perceptual adaptation - similar to that which is involved in adaptation to spatial misalignment (e.g. Redding & Wallace, 1993) and in adaptation to purely intersensory misalignment (e.g. Fujisaki, Shimojo, Kashino, & Nishida, 2004) - is also involved in this adaptive response. Following an attempted replication of Cunningham, Billock, and Tsou's (2001) study in Chapter 1, I present in this chapter two experiments that demonstrate that aftereffects of adaptation to temporal misalignment do not spontaneously decay. The literature on adaptation to spatial misalignment suggests that, while behavioural learning spontaneously decays in the absence of reinforcement, perceptual learning persists. Therefore these results were consistent with adaptation being effected through perceptual learning. However, a third experiment took explicit perceptual measures and found no direct evidence of a perceptual aftereffect at a group level.

In a replication of Cunningham, Billock and Tsou's (2001) experiment, I found a negative aftereffect, but it did not meet the criterion for significance (see Chapter 1). That aftereffects are not reliably detected with this procedure may be due to the insensitivity of the categorical aftereffect measure (crash rate) and to the availability of visual feedback in the post-test, which could cause the aftereffect rapidly to decay whether it is an aftereffect of behavioural or perceptual adaptation. Moreover, as discussed above, the procedure does not distinguish between perceptual and behavioural learning.

In this chapter, I present three experiments which used tasks that allowed the decay of aftereffects to be measured, one with visual feedback retained in the post-test, one without and, finally, one with the addition of purely perceptual measures. Since Cunningham, Billock, and Tsou's (2001) task was dependent on visual feedback, a new procedure had to be developed which could exclude visual feedback, yet allow behaviour to be measured. This problem has been addressed in research on adaptation to spatial misalignment. As outlined in Chapter 0, a typical experiment in this area involves placing prisms in front of the eyes to produce a lateral displacement of perceived visual space,pointing at a usually point-like visual stimulus. Feedback is withheld in the pre-test and post-test simply by obscuring the participants' vision of their arms but not of the visual stimulus (see Redding, Rossetti, & Wallace, 2005 for a review of prism adaptation research).

An equivalent procedure for temporal adaptation would need to address the need to give the stimulus temporal features and to temporally displace visual feedback, as well as obscuring the feedback in the pre- and post-tests. A regular periodic stimulus would provide the temporal characteristics to give participants a basis for timing their actions. In Experiments 2.0, 2.1, and 2.2, I used a pacing task based on these principles, with light emitting diodes (LEDs) serving as the periodic stimulus, and provided visual feedback using a laser spot slaved to the participant's movements. This was a form of feedback that could be delayed, and could be switched off as required. This procedure also permitted the acquisition of a more sensitive, continuous measure of aftereffects, expressed as a time interval, and to measure the decay of aftereffects. In Experiment 2.0, I retained Cunningham, Billock, and Tsou's (2001) and Experiment 1.0's use of feedback in the post-test, but in Experiment 2.1 there was no feedback in the post-test. As I argued in Chapter 0, one should expect perceptual adaptation to persist (in the absence of visual feedback), but behavioural adaptation to decay. Consistent with this, an aftereffect decayed in Experiment 2.0 and persisted in Experiment 2.1. Finally, in Experiment 2.2, perceptual aftereffects of adaptation were not detected.

Experiment 2.0: Temporal Adaptation Demonstrated With a New Paradigm

The hypothesis was that participants in the delay condition would have a more negative (negative = earlier response) pre-post shift in performance error than those in the control condition.

Method

Participants. Twenty participants were recruited from the paid participant panel at Cardiff University, and were each paid £2. The participants were randomly assigned to each of the two conditions.

Apparatus. The participant was seated on a chair, of adjustable height, with his or her chin resting in a chin-rest, with adjustable cheek-restraints, in a head-tracker that permitted only axial neck rotation movements to a maximum of 30 degrees left and right of straight ahead (see Figures 2.0 and 2.1 for line drawings of the apparatus). The head-tracker was suspended from a frame, and positioned such that the participant's eyes were 0.75 m from the wall. Two green LEDs were positioned on the wall in front of the participant, 30 degrees to the left and right of straight ahead.

The position of the head-tracker was sampled twice every millisecond, using a potentiometer, and recorded to a computer, running Microsoft Windows XP, through a National Instruments BNC-2090 adapter and a National Instruments PCI-6052E input-output (I/O) card. This system has input and output sampling rates of 333,000 samples per second. A red laser (class 3B) was positioned above and behind the participant's chair, with its beam directed towards the wall in front of the participant. Local permission was obtained for the use of the laser, and appropriate safety precautions were taken in the positioning of the laser and other equipment to ensure that the laser could not make contact with the participants' eyes. A mirror-galvanometer (Cambridge Technology, MA, USA) was used to deflect the laser beam to various positions on the wall, dependent on the positions of the head-tracker.

The Borland Delphi programming language, with National Instruments' DAQ-mx library, was used to control and record from the computer's I/O card. Specifically, it was used to turn the LEDs on and off, record head-tracker positions and determine laser positions.

Design. A two level, between-participants design was used. The independent variable was exposure (control | delay). The procedure consisted of three phases (pre-test | exposure | post-test). Participants' performance error was calculated in both the pre-test and the post-test. The dependent variable (total shift) was calculated as the post-test performance error minus the pre-test performance error.

Procedure. In the pre-test, two LEDs, 30 degrees to the left and right of straight ahead, flashed alternately at a rate of 1 Hz, and for a duration of 20 ms. Participants were told that a laser spot on the wall was controlled by their head movements to the left and right. They were told to pay attention to the first two flashes to determine their rate, and then, from the third flash on, match their head movements to the LEDs, such that the laser spot reached each LED while it was flashing. The delay between head-movements and laser-movements was estimated to be less than a millisecond: At any given moment the laser spot was projected on the wall directly straight ahead of the participant's head. The LEDs flashed a total of 40 times during each run of the criterion task. The position of the head-tracker was sampled and recorded every 0.5 ms.

In the exposure phase, for participants in the delay condition, the display and task were identical to those in the pre-test except that the LEDs flashed a total of 150 times and that there was a delay of 250 ms between head movements and laser movements. In other words, the laser spot was always projected on the wall at a point straight ahead of the position that the head-tracker was at 250 ms earlier. Participants in the control condition rested during the exposure phase for 150 seconds. The procedure in the post-test was identical to that for the pre-test for all participants.

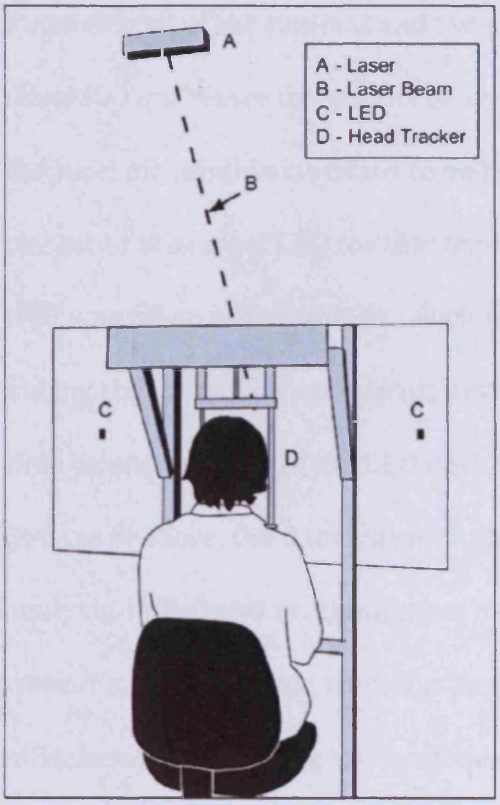

Figure 2.0. The laser and head tracker used in Experiments 2.0, 2.1, and 2.2 (rear view). The participant sat facing a wall, with two LEDs placed on the wall at thirty degrees to the left and right of straight ahead. In the exposure phase, the laser projected a spot of light on to the wall in front of the participant, and its movement was controlled by the participant's head movements.

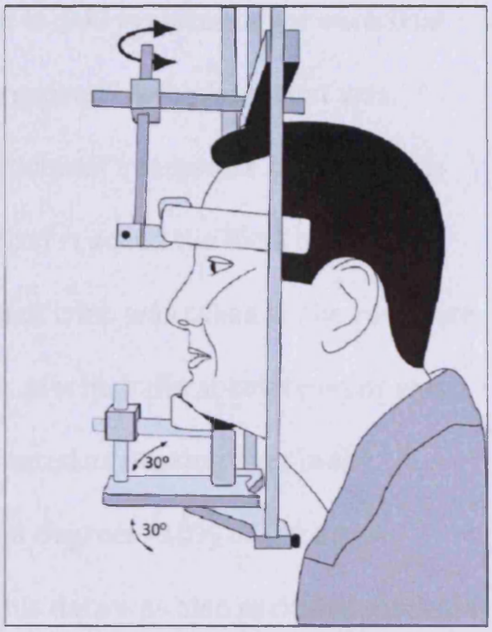

Figure 2.1. The head tracker used in Experiments 2.0, 2.1, and 2.2 (side view). The participant's head was constrained by chin- and cheek-rests, and the only possible neck movement was axial rotation up to thirty degrees left or right of straight ahead.

The raw sample data was converted into a measure of performance error for each trial of the pre-test and the post-test. A trial was defined as the period from 500 ms before the middle of an LED flash to 500 ms after it. For each trial, the local maximum was taken to be the point reached by the laser that was closest to the target LED for that trial. The participant's response time for each trial was taken as the time at which the laser first reached the local maximum during that trial. The participant's error, for each trial, was taken as the response time minus the time of the LED flash. For trials in which the absolute error was 500 ms or more, the data was excluded and treated as missing data in the analysis. If the local maximum was more than 6 degrees (10% of the head-tracker's range) distant from the target side, this data was also excluded, to avoid mistakenly interpreting the local maximum of a small task-irrelevant movement as a true attempt on trials where the participant had made no deliberate movement. The total shift, or aftereffect, was calculated as the median error during the post-test, minus the median error during the pre-test.

To obtain a measure of the decay of aftereffects for each participant, the following calculations were made. Because there was a tendency in all phases of both conditions for the first few trials to produce more positive errors than later trials, a participant's error (in milliseconds) for each trial of the pre-test was taken away from the error in the post-test trial that was in the same ordinal position within the phase to provide a measure of aftereffect for each trial in the post-test. To avoid measures of slope being biased by outliers, for each participant aftereffects were ranked, and a linear regression in terms of trial was conducted on the ranked data. The coefficient of trial in the resulting regression equation was taken as a measure of slope. More positive slopes indicated a tendency for the negative aftereffect to diminish over the course of the post-test.

Because the sample size was relatively small, normality tests would have lacked the power to detect deviations from normality. Thus, non-parametric statistics were used throughout Experiments 2.0 and 2.1.

Results and Discussion

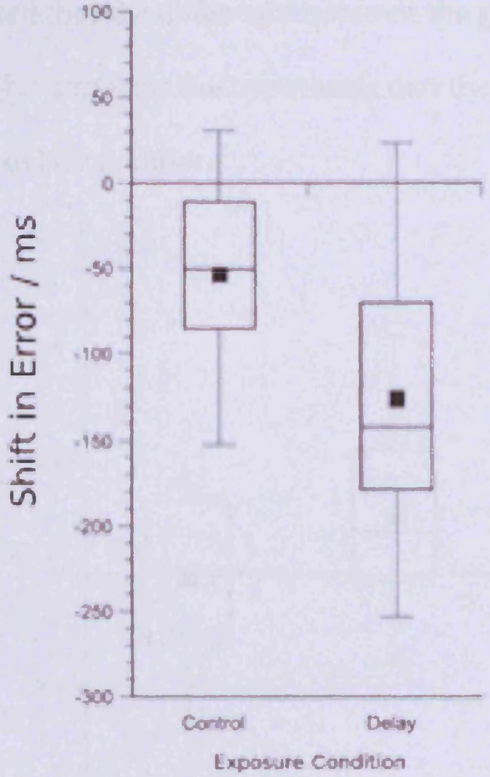

Figure 2.2. Box and whiskers plot of the effect of exposure to delay on the median pre-post shift in error in Experiment 2.0. The box represents the median and the first and third quartiles, and the whiskers extend as far as the minimum and maximum values after outliers (values more than 1.5 interquartile ranges below the lower quartile or above the upper quartile) are excluded. The filled black

square indicates the arithmetic mean. More negative values indicate adaptive aftereffects (early movements) in the post-test, compared with the pre-test.

The median total shift (with interquartile range in parentheses) for the control group was -50 (-82 to -13) ms, and the median total shift for the delay group was -140 (-172 to -72) ms (see Figure 2.2). Thus, the total effect of exposure was (-140 ms - -50 ms =) -90 ms, which amounted to a total shift of 37% of the induced temporal displacement. An independent samples Mann-Whitney *U* test indicated that the difference between the groups was significant, *U*(18) = 26, $p = 0.04$. This supports the hypothesis that there would be more negative errors in the delay condition.

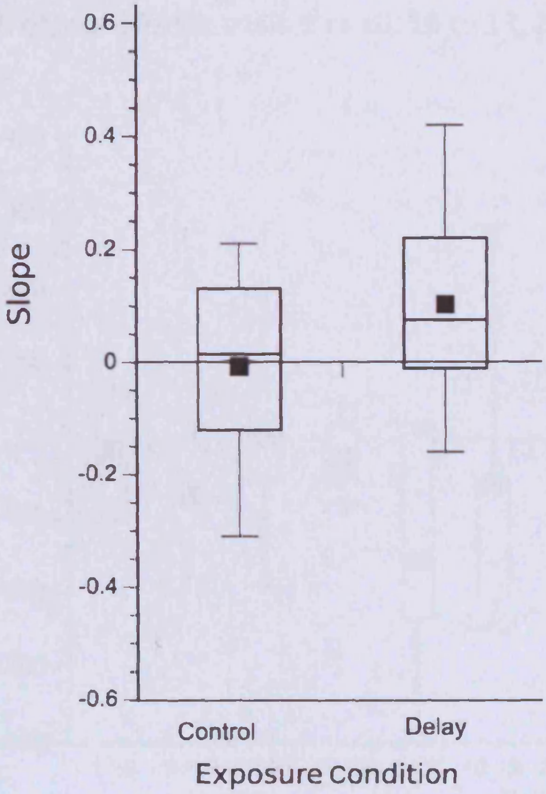

Figure 2.3. Box and whiskers plot of slope in Experiment 2.0 as measured by a regression of ranked aftereffect over trial. More positive values indicate that

adaptive aftereffects (early movements) tended to wane over the course of the post-test, compared with the pre-test.

The median slope (with interquartile range in parentheses) in the control condition was 0.02 (-0.09 to 0.12), and in the delay condition it was 0.08 (-0.002 to 0.20) (see Figure 2.3). A Wilcoxon signed-rank test was applied for each condition to investigate whether there was a positive slope (i.e. a decay of aftereffects). The slope in the control condition was not significantly greater than zero, $Z(9) = 0.3$, $p = 0.4$. The slope in the delay condition was greater than zero, but marginally non-significant, $Z(9) = 1.5$, $p = 0.06$. Figure 2.4 shows the aftereffects in each of four blocks: trials 1 to 10, 10 to 19, 20 to 29 and 29 to 38.

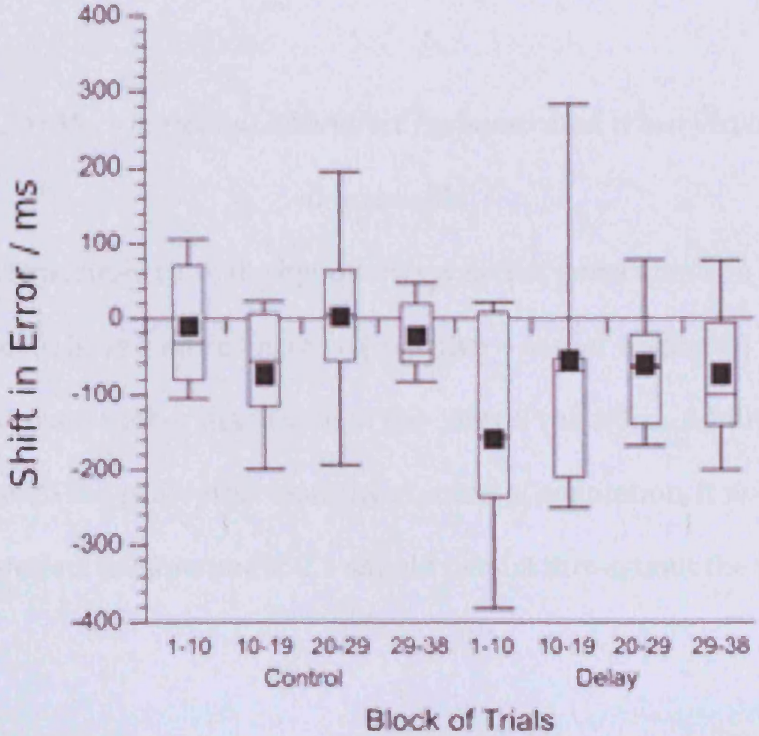

Figure 2.4. Box and whiskers plot of the median pre-post shift in error in Experiment 2.0, for each of four blocks of trials: 1 to 10, 10 to 19, 20 to 29, and

29 to 38. More negative values indicate adaptive aftereffects (early movements) in the post-test, compared with the pre-test.

Experiment 2.0, then, produced a significant behavioural aftereffect of adaptation, in the predicted direction, and it waned over the course of the post-test. Since visual feedback was available during the post-test, the participants were aware of any errors and could correct them, even in the face of a persistent perceptual aftereffect. Thus, Experiment 2.1 was designed to replicate Experiment 2.0 but with no visual feedback in the test phases. This manipulation was of interest for its potential to address the question of whether the aftereffect was due to the persistence of behavioural responses learnt during the exposure phase or due to perceptual learning.

Experiment 2.1: More Persistent Aftereffect Demonstrated When Visual Feedback is Unavailable

As in Experiment 2.0, the hypothesis was that participants in the delay condition would have a more negative (negative = earlier response) pre-post shift in performance error than those in the control condition. Additionally, in accordance with the perceptual learning account of adaptation, it was predicted that the aftereffect in Experiment 2.1 should persist throughout the post-test.

Method

Apparatus, design, and procedure. As Experiment 2.0, except that the laser spot was switched off during the pre- and post- tests. Participants' instructions for these phases were modified to require them to time head movements to coincide with the LED flashes, rather than requiring them to time the laser spot to coincide with the LED flashes.

Results

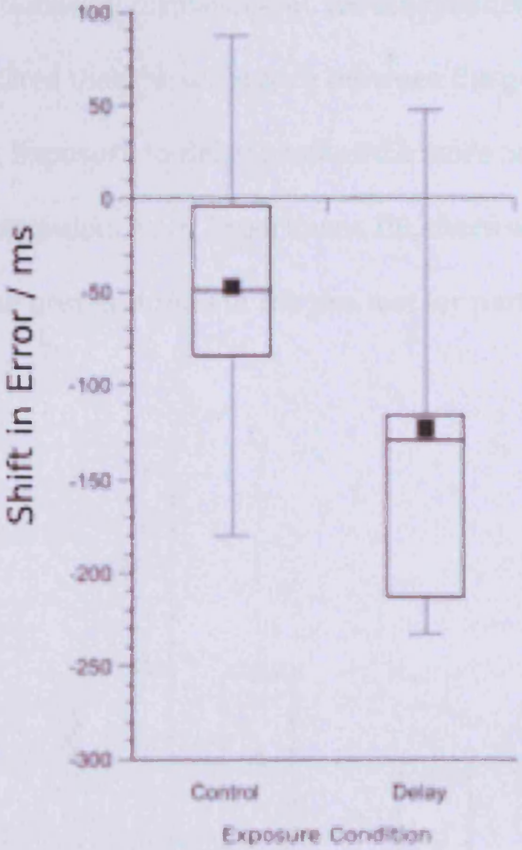

Figure 2.5. Box and whiskers plot of the effect of exposure to delay on the median pre-post shift in error in Experiment 2.1. The box represents the median and the first and third quartiles, and the whiskers extend as far as the minimum and maximum values after outliers (values more than 1.5 interquartile ranges below the lower quartile or above the upper quartile) are excluded. The filled black square indicates the arithmetic mean. More negative values indicate adaptive aftereffects (early movements) in the post-test, compared with the pre-test.

The median total shift (with interquartile range in parentheses) for the control group was -49 (-78 to -8) ms, and the median total shift for the delay group was -130 (-210 to -120) ms (see Figure 2.5). Thus the total effect of exposure was (-130 ms - -49 ms =) -81 ms, which amounted to a total shift of 32% of the induced temporal displacement. An independent samples Mann-Whitney *U* test indicated that the difference between the groups was significant, $U(18) = 26, p = 0.04$. Exposure to delay produced a more negative aftereffect than in the control condition. As in Experiment 2.0, there was a shift to more negative errors in the post-test than in the pre-test for participants exposed to the delay.

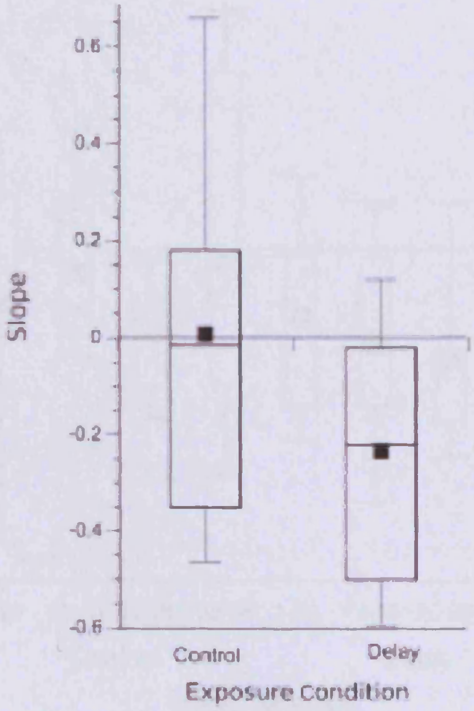

Figure 2.6. Box and whiskers plot of slope in Experiment 2.1 as measured by a regression of ranked aftereffect over trial. More positive values indicate that adaptive aftereffects (early movements) tended to wane over the course of the post-test, compared with the pre-test.

The median slope (with interquartile range in parentheses) in the control condition was -0.02 (-0.34 to 0.18), while in the delay condition it was -0.22 (-0.47 to -0.03) (see Figure 2.6). A Wilcoxon signed-rank test was applied for each condition to investigate whether there was a positive slope (i.e. a decay of aftereffects). The slope in the control condition was not significantly greater than zero, $Z(9) = -0.1$, $p = 0.50$. The slope in the delay condition was also not significantly greater than zero, $Z(9) = -2.1$, $p = 0.98$. Figure 2.7 shows the aftereffects in each of four blocks: trials 1 to 10, 10 to 19, 20 to 29 and 29 to 38.

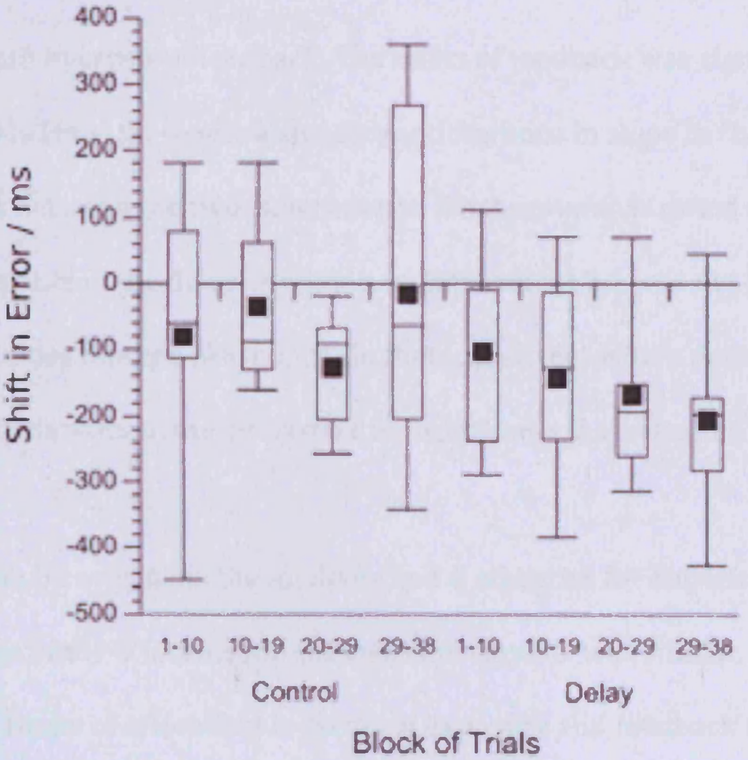

Figure 2.7. Box and whiskers plot of the median pre-post shift in error in Experiment 2.1, for each of four blocks of trials: 1 to 10, 10 to 19, 20 to 29, and 29 to 38. More negative values indicate adaptive aftereffects (early movements) in the post-test, compared with the pre-test.

Comparison of Experiments 2.0 and 2.1. I conducted a 2x2 ANOVA of ranks, using Puri and Sen's (1985; and see Thomas, Nelson & Thomas, 1999, for a review of its application to behavioural sciences) L statistic, on slope in terms of exposure (delay | control) and feedback (feedback | no feedback). The adjusted R^2 for the model was 0.16, and the model was significant, $L(3) = 8.6$, $p < 0.05$. There was a significant interaction between exposure and feedback conditions, $L(1) = 4.9$, $p < 0.05$. To test the hypothesis that the aftereffect decayed more slowly in the absence of feedback than with visual feedback, a one-tailed Mann-Whitney's U test was conducted, on the data for the delay conditions only, on slope of shift in terms of feedback. The effect of feedback was significant, $U(18) = 14$, $p = 0.01$. Thus, there was a significant difference in slope in the delay conditions between the two experiments. Furthermore, as noted above, the slope for participants in the delay condition in Experiment 2.1 was not greater than zero. Therefore one can also conclude that, consistent with a perceptual learning account of adaptation, the aftereffect in Experiment 2.1 persisted throughout the post-test.

As can be seen from the medians and U statistics for Experiments 2.0 and 2.1, the size of the aftereffect in the two experiments was similar. Indeed, a 2x2 ANOVA of ranks of aftereffect in terms of exposure and feedback showed that there was no interaction, $L(1) = 0.003$, $p > 0.9$). This result was surprising. Because the aftereffect persisted in Experiment 2.1 and decayed in Experiment 2.0, an equivalent initial aftereffect should, in Experiment 2.1, have produced a larger median aftereffect over the course of the post-test. However, note that the slope in Experiment 2.1's delay condition was negative (see Figure 2.6), and that the measured aftereffect was close to zero in the first ten trials of the post-test (see Figure 2.7). Indeed, the slope of aftereffects in Experiment 2.1 was marginally non-significantly less than zero, $t(9) = -2.192, p = 0.056$. I cannot be certain of the cause of this apparent suppression of the aftereffect at the start of the post-test in the absence of feedback and gradual increase in it over the course of the post-test, but I offer a speculative account of it below.

Interim Discussion

Experiment 2.0 used a new paradigm that was sensitive to aftereffects and able to provide a trial-by-trial measure of temporal error. In this experiment there was a significant aftereffect of adaptation to delayed visual feedback, which decreased over the course of the post-test. Experiment 2.1 eliminated visual feedback from the pre- and post-test phases and produced an aftereffect of similar median size to that in Experiment 2.0, but which persisted for the 40 seconds of the post-test.

The persistence of the aftereffect in the absence of visual feedback is consistent with the adaptation being solely due to perceptual learning. In Experiment 2.0, there was clear visual performance feedback to inform the participant that they were making an error. This information would be available whether perceptual learning, behavioural learning, or both had occurred, since the error signal is generated by the discrepancy between two visual stimuli: the LED and the laser-spot. Conversely, in Experiment 2.1, the only available performance feedback would be the error between the perceived timing of the head movement and the perceived timing of the LED flashes. If the aftereffect were the result of perceptual learning, any resulting error between the head movements and the LED flashes would not be perceived as an error. If the aftereffect were due to transfer of behavioural learning, and no perceptual adaptation had happened, the objective error would be detected. The slope might be less steeply positive than in Experiment 2.0, since an inter-sensory error may be less salient than an intra-sensory error. However, that the slope in Experiment 2.1 was close to zero, and was not greater than zero ($p = 0.98$), is consistent with behavioural learning not being solely responsible for the aftereffect.

Problems with Interpreting the Rate of Decay

Nonetheless, it cannot be ruled out that the aftereffect was due to behavioural learning and that the resulting visuomotor performance error was insufficiently salient to prevent persistence, or that the rate of readaptation was too slow to be noted within the 40 seconds of the post-test. Furthermore, I know of no indication from the literature as to the expected rate of spontaneous decay of behavioural learning in a task like the one used in Experiment 2.1, and it is thus difficult to infer whether 40 seconds would have been a sufficient period of time over which to detect the decay of behavioural learning.

It should also be noted that perceptual readaptation could, under some circumstances, occur in the post-test of Experiment 2.1, despite the lack of visual feedback of motor actions. Even though there was no performance error feedback (assuming visual and motor representations were perceptually adapted), there may, if the head-neck proprioceptive system had adapted more or less than the head-neck motor system, have been intrasystem misalignment in the head-neck sensorimotor system, motivating partial readaptation, as in Choe and Welch's (1974) prism adaptation experiment.

However, whereas a behavioural learning account would predict full decay eventually by means of extinction, a perceptual learning account would predict no decay or – if adaptation is unevenly distributed in the proprioceptive-motor system – partial decay; and so the apparent absence of any decay in Experiment 2.1 is more consistent with perceptual learning than with behavioural learning.

Increasing Aftereffects in the Absence of Feedback.

I argued that a behavioural learning account of adaptation would predict a decay of aftereffects, due to either or both of extinction and relearning from information acquired by comparing efference or proprioceptive information with visual target information; whereas a perceptual account would predict that there would be no change over time, until any new conflicting information was obtained (e.g. non-delayed feedback). In fact, inconsistent with both these accounts, aftereffects appeared to increase after the removal of the delayed feedback, albeit marginally non-significantly. An explanation for this may lie in the relatively slow time-course of perceptual adaptation, compared with behavioural adaptation.

A system for adapting behaviour or perception to cope with changeable neural delays, environmental demands and performance error could respond immediately to incoming data, or could be more conservative, waiting to receive a number of samples before deciding its output. The former would allow more rapid adaptation and would be flexible and sensitive to sudden changes in its inputs; whereas the latter would produce smoother changes in output, even if it had a sudden change in its input, and would therefore be slow to respond and insensitive to brief changes in its inputs.

World learning in a visuomotor coordination task would be more useful the more rapid it was. Such task-specific world learning should be able to respond quickly to unexpected performance errors, as they may appear suddenly and need immediate correction. Conversely, perceptual learning would be unreliable if it were to respond to every apparent error immediately. Normal imprecision in the visual percept, the efference copy, or the execution of the motor command could produce frequent and variable apparent errors between expected and perceived locations: If the interpretation of sensory input were altered immediately in response to such errors, they would never be detected or corrected for behaviourally and both an unstable perceptual world and uncorrected behavioural imprecision would obtain.

Indeed, in adaptation to spatial misalignment, perceptual adaptation does develop more slowly than behavioural correction of performance error (e.g. Redding & Wallace, 1993). A possible consequence of this slow response in perceptual learning is that, while behavioural aftereffects of adaptation may extinguish in the absence of further (confirmatory or contradictory) information, perceptual aftereffects may continue to grow for a while.

Doing the pre-test and post-test (with no feedback) should have no effect on the relationship among the involved systems, since there is no visuomotor feedback occurring during those times. The relationship may be affected by rearranged feedback during the exposure phase, and normal feedback during whatever visuomotor activities participants were engaged in before they came into the laboratory. At the start of the post-test, normal feedback is a more recent experience (and thus, perhaps, more highly weighted in deciding any corrections to perception) than it is at the end of the post-test; so any effect of the prior normal feedback on perceptual alignment should wane over the course of the post-test, producing an increase in perceptual aftereffects.

Indeed, the apparent increase in aftereffect following exposure found in Experiment 2.1 parallels similar results in adaptation to spatial (prismatic) misalignment. Templeton, Howard and Wilkinson (1974) found that, in participants whose visual perception was altered by exposure to spatial misalignment, the visual aftereffects increased over the course of 7 minutes of post-exposure testing. Choe and Welch (1974) also reported non-significant increases in visual aftereffects, over 15 minutes of testing after prism exposure.

The non-significantly increasing aftereffect in these results, which is more consistent with a perceptual learning account that produces immediate correction than with a behavioural account, may be *most* consistent with a perceptual learning account that predicts smoothed changes in alignment. However, I emphasize that this is a speculative interpretation, and the claim that these results reflect perceptual adaptation is tested more directly in Experiment 2.2, below, by replicating these findings with the addition of purely perceptual measures of perceptual adaptation.

Problems with Choosing an Appropriate Size for the Visuomotor Misalignment

The visuomotor misalignments used in this paper have been, like the delays used in previous studies of temporal adaptation (e.g., Cunningham, Billock, & Tsou, 2001; Cunningham, Chatziastros, et al., 2001; Miall & Jackson, 2006; and

Pesavento & Schlag, 2006), of the order of several hundreds of milliseconds. Developmental changes in sensorimotor neural transmission have been reported only of the order of tens of milliseconds, and I am not aware even of environmental changes that produce changes in lag of greater than 100 milliseconds. Thus, even if an experiment demonstrated no perceptual aftereffects of exposure to, say, 200 millisecond lags, one could argue that this might have been because the lags were outwith the range of lags with which the involved systems are evolved to cope.

It is possible that researchers in this field have erred on the side of long exposed lags for two reasons: A given percentage aftereffect of a longer lag may be statistically more easily detectable, given a constant amount of variance; and early research on this subject (Lee, 1950a) suggested that performance was affected more by longer lags. However, more recent research that has measured aftereffects, rather than just the delay's direct effect on performance, after explicitly manipulating the length of the exposed lags (Stetson et al., 2006) suggests that shorter lags (100 ms) produce larger aftereffects than longer lags (250 ms or longer). Future research should, therefore, investigate in more detail the effects of manipulating the length of the lag on adaptation and on aftereffects of adaptation, and should take care not to use only lags of several hundreds of milliseconds.

Further Directions for Investigating Temporal Adaptation

The paradigm used in Experiments 2.0 and 2.1 can be modified in various ways to investigate further the nature of temporal adaptation. I have shown that it can be used to produce and detect behavioural aftereffects, as well as allowing quantitative measurement of the aftereffects as a time interval, and enabling the measurement of decay of aftereffects. The limitations discussed above could be addressed by using a longer post-test; by introducing a period of inactivity before the post-test, varied between subjects (as in Fernandez-Ruiz et al., 2004) to rule out perceptual readaptation due to proprioceptive-motor intrasystem misalignment; and by introducing a new condition in which veridical visual feedback of motor actions is given, but behaviour is modified via performance feedback (as in Bedford, 1993b).

Thus far, I have focused on distinguishing between perceptual and behavioural adaptation in terms of their decay, while retaining behavioural post-test measures that confound perceptual and behavioural adaptation in themselves (as in other studies of temporal adaptation, e.g., Cunningham, Billock, & Tsou, 2001; Cunningham, Chatziastros, et al., 2001; and Pesavento & Schlag, 2006). Alternative approaches to distinguishing perceptual and behavioural adaptation could be pursued by retaining the exposure task introduced in this paper but replacing the pre-test and post-test measures with perceptual measures, such as temporal order judgments and the stream-bounce task used in Fujisaki et al.'s (2004) experiments. If such experiments produced direct evidence of perceptual adaptation, one could additionally, by using different response and stimulus modalities in the pre- and post-test tasks, such as an auditory timing stimulus or a finger tapping response, begin to identify factors affecting the localization of aftereffects across the involved sensorimotor systems.

Experiment 2.2: Perceptual Aftereffects of Adaptation Not Detected

As in Experiments 2.0 and 2.1, the hypothesis was that participants in the delay condition would have a more negative (negative = earlier response) pre-post shift in performance error than those in the control condition. Additionally, in accordance with the perceptual learning account of adaptation, it was predicted that the aftereffect in Experiment 2.2 should persist throughout the post-test, just as in Experiment 2.1. Finally, I predicted that there should be a more positive (positive = visual events perceived earlier) pre-post shift in point of subjective visuomotor simultaneity in the delay condition than in the control condition.

Method.

Participants. Pilot data indicated relatively high variance in the perceptual aftereffect variable, so a larger sample was taken in this experiment to increase power. Forty participants were recruited from the paid participant panel at Cardiff University, and were each paid £3. The participants were randomly assigned to each of the two conditions.

Apparatus, design, and procedure. As in Experiment 2.1, except that a temporal order judgment phase was added before the pre-test behavioural phase and before the post-test behavioural phase.

Temporal order judgment task. During each trial, participants were presented with a visuomotor asynchrony, chosen by the staircase method. Two interleaved staircases were used, with one starting at a +200 asynchrony, and the other starting at a -200 asynchrony. The step size was 100 ms (although, because of the variable nature of participants' motor actions, the psychometric function was sampled with a finer grain than that would imply) and each staircase terminated after 10 reversals.

Participants were asked to judge whether the motor or the visual component was first. At the start of each trial, one of the two LEDs flashed, to indicate the direction of motor action that would be required. Participants were asked to make a head movement away from straight ahead, to the furthest point in the direction of the LED, and back to straight ahead, between two beeps which were separated by 1200 ms. Meanwhile, the LED in that direction flashed for a second time. Participants were asked to compare the time that their head was at the point furthest from centre with the time that the LED flashed for the second time. The timing of the LED flash was placed relative to the arithmetic mean of the participant's five most recent motor timings, and the actually achieved asynchrony was recorded. A measure of visuomotor alignment was obtained from the pre-test and the post-test separately, by calculating the parameters of a probit function of response in terms of actual asynchrony; the resulting point of subjective simultaneity (PSS) was positive if participants required the visual event to be objectively later to appear simultaneous. Finally, a measure of perceptual adaptation (shift of PSS) was obtained by taking the post-test PSS minus the pre-test PSS. Thus, the adaptive direction for this measure was for it to be positive.

Results and Discussion

With a larger sample than Experiments 2.0 and 2.1, it was possible to assess whether there were deviations from normality: there were no significant deviations from normal skew and kurtosis, after exclusion of outliers. However, to retain comparability with the earlier experiments, non-parametric statistics were still used. The median behavioural aftereffect (with interquartile range in parentheses) for the control group was -32 (-87 to 22) ms, and the median behavioural shift for the delay group was -40 (-112 to -1) ms (see Figure 2.8). Thus the total effect of exposure was (-32 ms - -40 ms =) -8 ms, which amounted to a total aftereffect of 3% of the induced temporal displacement. An independent samples Mann-Whitney *U* test indicated that the difference between the groups was not significant, $U(38) = 170, p = 0.41$.

As in Experiments 2.0 and 2.1, there was a shift to more negative errors in the post-test than in the pre-test for participants exposed to the delay, but this was non-significant and of a size very much smaller than was found in Experiment 2.1. A post-hoc power analysis indicated that a 40% aftereffect (typical of aftereffects found in both the spatial and the temporal literature) of 100 ms would have been detectable, with power of .96.

The median slope (with interquartile range in parentheses) in the control condition was -0.02 (-0.08 to 0.01), while in the delay condition it was 0.07 (-0.05 to 0.23) (see Figure 2.9). A Mann-Whitney *U* test indicated that there was a marginally non-significant difference between the two groups, $U(34) = 100, p = 0.06$. A Wilcoxon signed-rank test was applied for each condition to investigate whether, for each group, aftereffects changed over the course of the post-test. The slope in the control condition was not significantly different from zero, $Z(15) = -1.6, p = .12$. The slope in the delay condition was marginally non-significantly different from zero, $Z(19) = 1.8, p = .07$. Thus, there was a trend for negative behavioural aftereffects in the delay condition to decay over the course of the ms, and the median behavioural aftereffect for the delay group was -17 (-77 to 72) ms (see Figure 2.10). Thus the total effect of exposure was (-17 ms - -41 ms =) +24 ms, which amounted to a total aftereffect of 10% of the induced temporal displacement, but in the maladaptive direction. An independent samples Mann-Whitney *U* test indicated that the difference between the groups was not significant, *U*(36) = 143, *p* = .29.

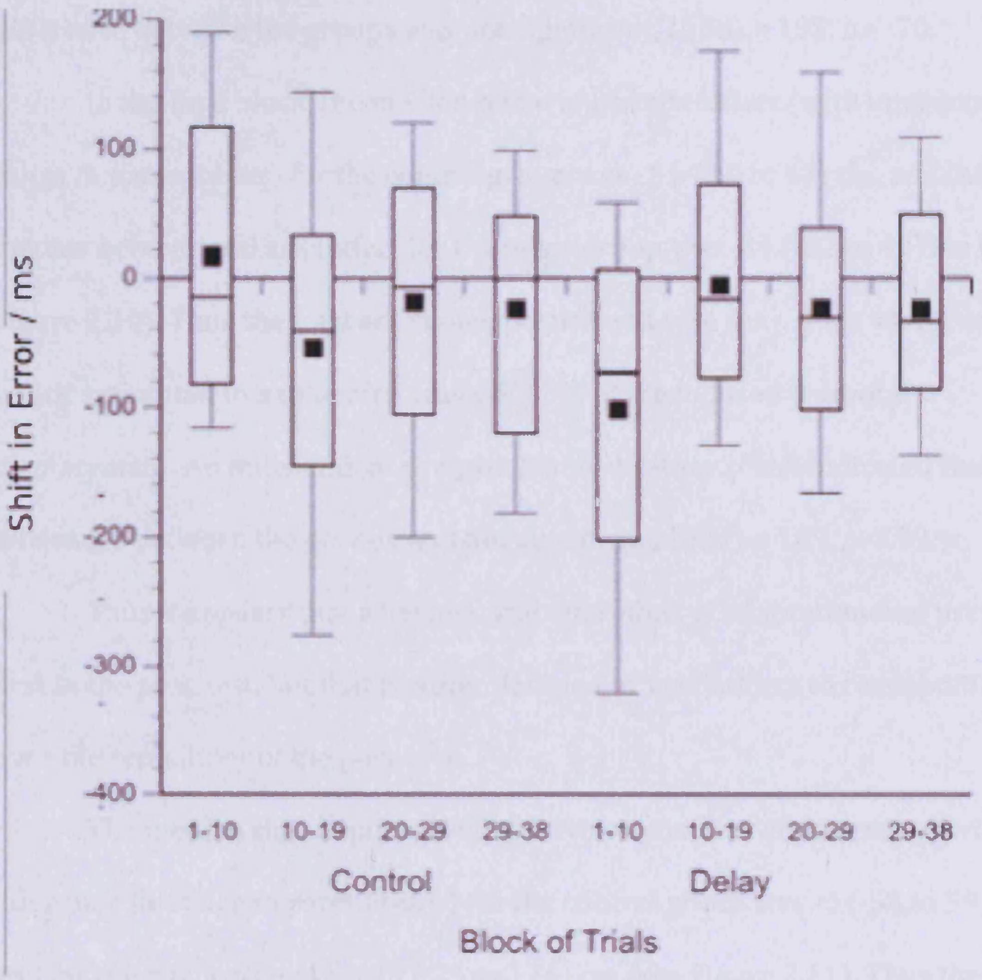

Figure 2.10. Box and whiskers plot of the median behavioural aftereffect in Experiment 2.2, for each of four blocks of trials: 1 to 10, 10 to 19, 20 to 29, and 29 to 38. More negative values indicate adaptive aftereffects (early movements) in the post-test, compared with the pre-test.

In the third block, the median behavioural aftereffect (with interquartile range in parentheses) for the control group was -8 (-106 to 69) ms, and the median behavioural aftereffect for the delay group was -32 (-102 to 38) ms (see Figure 2.10). Thus the total effect of exposure was (-32 ms - -8 ms =) -24 ms, which amounted to a total aftereffect of 10% of the induced temporal displacement. An independent samples Mann-Whitney *U* test indicated that the difference between the groups was not significant, *U*(38) = 185, *p* = .70.

In the final block, the median behavioural aftereffect (with interquartile range in parentheses) for the control group was -1 (-120 to 47) ms, and the median behavioural aftereffect for the delay group was -34 (-82 to 40) ms (see Figure 2.10). Thus the total effect of exposure was (-34 ms - -1 ms =) -33 ms, which amounted to a total aftereffect of 13% of the induced temporal displacement. An independent samples Mann-Whitney *U* test indicated that the difference between the groups was not significant, *U*(37) = 189, *p* = .99.

Thus it appears that a behavioural aftereffect of adaptation was present at first in the post-test, but that it either decayed or was subject to readaptation over the remainder of the post-test.

The median shift in point of subjective visuomotor simultaneity (with interquartile range in parentheses) for the control group was -6 (-58 to 59) ms, and for the delay group was 25 (-25 to 124) ms (see Figure 2.11). Thus the total effect of exposure was (25 - -6 ms =) 31 ms, which amounted to a total aftereffect of 12% of the induced temporal displacement. An independent samples Mann-Whitney *U* test indicated that the difference between the groups was not significant, *U*(36) = 141, *p* = 0.26. A post-hoc power analysis indicated that a 40%

aftereffect (typical of aftereffects found in both the spatial and the temporal literature) of 100 ms would have been detectable, with power of .85.

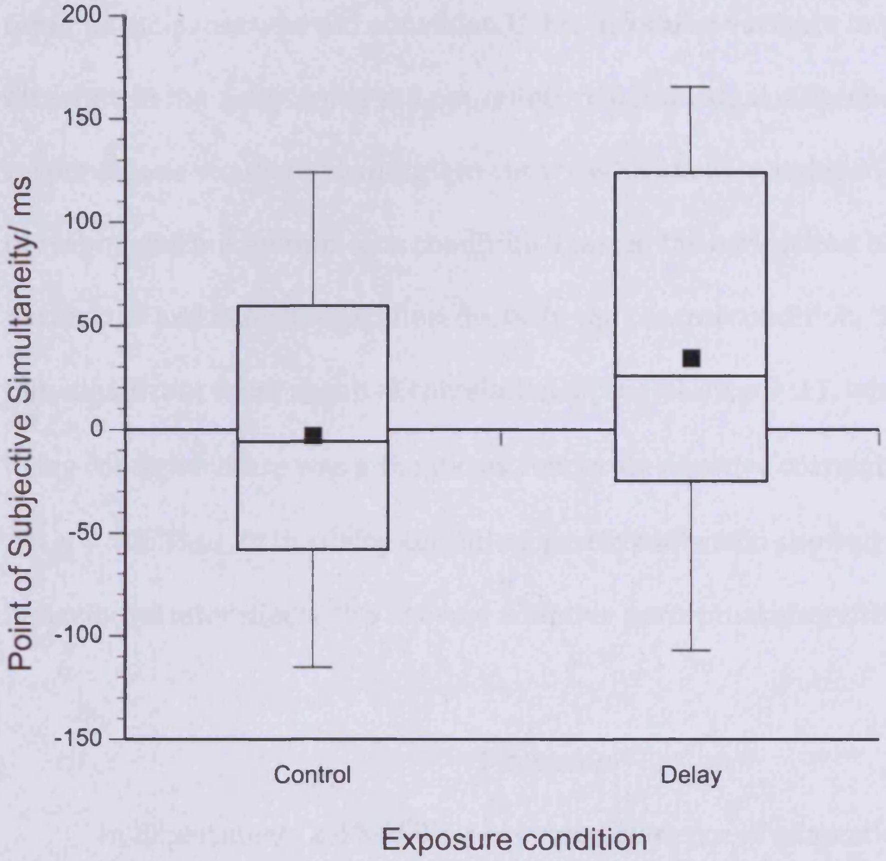

Figure 2.11. Box and whiskers plot of the median perceptual aftereffect in Experiment 2.2. More positive numbers indicate that visual events had to be objectively later in order to be judged simultaneous; this being the direction of shift which would be adaptive in response to objective delayed visual feedback.

Inspection of the data for the perceptual aftereffects showed that, although there was no significant difference between the control and the delay groups, there was a notably larger difference in the third quartile (59 *vs* 124 ms) than in the first quartile (-58 vs -25 ms) or the median (see Figure 2.11), suggesting that a subset of participants in the delay condition showed a perceptual aftereffect, but that this may have been obscured by the presence of other participants who did not adapt. If this increased variance in the adaptive direction in the delay group did not reflect real individual differences in response, one would not expect it to covary with another, independent measure of response. Thus, within each condition, I tested the correlation between the perceptual and behavioural aftereffects. In the control condition, there was a non-significant weak negative correlation, $\rho(16) = -.39$, $p = .11$, whereas in the delay condition there was a significant moderate negative correlation, $\rho(18) = -.50$, $p = .02$. Thus, in the delay condition, participants who showed adaptive behavioural aftereffects also showed adaptive perceptual aftereffects.

Discussion

In Experiments 2.0 and 2.1, I provided evidence of adaptation to visuomotor temporal asynchrony in a predictable pacing task designed to facilitate comparison with the traditional pointing tasks of the prism adaptation literature. Results from these experiments were suggestive of perceptual change, as a behavioural aftereffect was detected that did not decay over the course of the post-test, and which indeed appeared to increase over that period. Experiment 2.2 replicated and extended Experiment 2.1 to test for perceptual effects more directly, by using visuomotor perceptual criterion tasks before and after exposure to visuomotor misalignment. The results of Experiment 2.2 indicate that, at the group level, perceptual adaptation had not taken place, as there was no pre-post difference in the point of subjective visuomotor simultaneity. Furthermore, the behavioural aftereffects measures that, in

Experiment 2.1, appeared to indicate a persistent aftereffect, detected in Experiment 2.2 a significant aftereffect only in the first 10 trials of the post-test, when taken following the temporal order judgment task. However, the overall behavioural aftereffect was correlated with the perceptual aftereffect measure, suggesting that the lack of significant perceptual aftereffects in the group data may reflect individual differences in responses to the delayed visual feedback.

One possibility, noted in the Interim Discussion, above, is that aftereffects may wane as a result of motor-proprioceptive perceptual readaptation, if participants are engaged in motor activity (in the absence of visual feedback), as indeed they were during the temporal order judgment tasks, and if the exposure-induced perceptual adaptation were confined to one part of the proprioceptive-motor system. However, the apparently decayed behavioural aftereffects, combined with the absence of perceptual aftereffects, is more consistent with the adaptation having been effected behaviourally in the first place. Thus, the most reasonable conclusion to be drawn from these experiments as a whole is that participants can adapt behaviourally in this task, and that behavioural aftereffects persist for at least 40 seconds, in the absence of new visuomotor alignment information, but that they wane thereafter, as would be expected of behavioural learning.

One must then consider why participants adapted behaviourally but not perceptually to the exposure task used in this chapter. The procedure shared many features with typical exposure tasks used in spatial adaptation, translated into the temporal domain. Thus, where in a prism adaptation task participants have a spatially punctuate target, and make a motor action designed to coincide spatially with that target, in the present task participants had a temporally punctuate target (an LED flash), and made motor actions designed to coincide temporally with that target. In these respects, at least, the procedure conformed to typical prism exposure tasks. However, in one respect, it differed from the norm. In prism adaptation, continuous visual feedback of limb position, from its start point to its end point, increases the behavioural and reduces the perceptual component of adaptation (Redding & Wallace, 1997b), relative to exposure conditions in which the error is available to the participant only after the movement has begun.

How then to adapt the terminal exposure paradigm for a temporal task? In a spatial task, terminal exposure ensures that the relative spatial error between the effector and the target is not known until the action has been completed, and that the participant cannot use relative error signals within a single modality (vision) as the basis for action (Redding & Wallace, 1997a). Clearly, a temporal error is unlike a spatial error in that it cannot be observed directly in a single temporal sample, nor can it be held in position and observed after the removal of an occluder. One solution might be to take advantage of the naturally occurring spatiotemporal occlusion afforded by oculomotor saccades (e.g. see Ross, Morrone, & Burr, 2001). In the procedure used in this chapter, visual feedback was always predictably approximately straight ahead of the participant's head, as the participants used their heads to perform the actions; and the visual targets were always in the same spatial location. If a task were used in which the visual feedback were visual feedback of hand movements on a computer screen, and if the target's position were not predictable, participants would be more likely to produce normal saccadic behaviour, thus providing natural discontinuities in the visuomotor feedback. An additional possible problem with the current procedure is that, with an entirely predictable target, a mere shift in the phase of the behaviour would suffice to resolve the performance error, without altering perception. A less predictable target would make such a simple behavioural solution impossible.

Summary

In summary, I presented a new paradigm that is sensitive to aftereffects of adaptation to sensory-motor temporal misalignment, and that is capable of measuring the size of the aftereffects and their rate of decay. With this paradigm, a visuomotor behavioural aftereffect of exposure to delayed visuomotor feedback was detected. Moreover, when performance feedback was unavailable in the post-test the aftereffect persisted for the duration of the post-test, suggesting that perceptual learning may have occurred. However, the addition of perceptual measures in a third experiment indicated that perceptual learning had not occurred at a group level, although correlational analysis suggested some participants may have adapted perceptually.

Chapter 3: Behavioural Adaptation in Continuous Visuomotor Tracking

In the previous chapter, I presented results suggesting that, in a simple visuomotor coordination task, behavioural but not perceptual adaptation is evoked. In the present chapter, the exposure task was a partial replication of Miall and Jackson's (2006) continuous unpredictable tracking task, and I extended it to assess perceptual change by administering visuomotor temporal order judgment tasks before and after exposure to delayed feedback. As in Miall and Jackson's (2006) study, there was no behavioural evidence of adaptation to a 300 ms delay; I found no evidence of perceptual adaptation either. Further manipulations, reducing the size of the delay and the predictability of the target trajectory, and introducing the delay gradually, led to behavioural adaptation, but still no perceptual adaptation. I argue that these results may suggest an inherent difference between the nature of the response to temporal and spatial misalignments.

In Chapter 2, I presented results suggesting that the adaptation demonstrated in Kennedy, Buehner, and Rushton's (2009) experiments (Experiments 2.0 and 2.1 in the present work) was not perceptual in nature. Several features of the exposure task may have impeded perceptual adaptation in this experiment. The simple predictability of the temporally punctuate alternation of left and right flashes at fixed locations meant that participants could simply adopt a strategy of behavioural anticipation which would immediately remove any performance error. Furthermore, the predominance of relatively constant velocity movement in the behaviour of participants in this task (aside from during the reversal points, which typically occurred around the time of a flash) would have reduced the salience of any visuomotor misalignment error, since temporal error has no impact on a constant velocity (or any constant parameter). Finally, the simplicity of the target (two alternating flashes) combined with the regularity of the motor behaviour required would have allowed the participant to attend to the visual feedback of their own motor actions continuously throughout the task. Furthermore, because the feedback consisted of a visual stimulus straight ahead or close to straight ahead of the participant's head, little or no eye movement would have been required to maintain fixation on the visual feedback at all times. In adaptation to spatial misalignment, continuous visual feedback of the hand tends to reduce perceptual adaptation in favour of behavioural adaptation to the misalignment, compared with terminal exposure in which the hand is visible only at the end of the movement (Redding & Wallace, 1997a). Thus, the ease with which participants could have attended to the visual feedback of the motor actions continuously could have prevented perceptual adaptation in the experiments described in Chapter 2.

Thus, in the experiments reported in the present chapter, I used the exposure task from Miall and Jackson's (2006) study, and variants on it. This was a tracking task, in which a target moved smoothly but not predictably around a two dimensional trajectory on a computer screen, while participants used a joystick to control the movements of a cursor. Participants were asked to track the target with the cursor. As well as preventing a mere behavioural phaseshifting solution by providing a less than completely predictable target (in contrast both to Cunningham, Billock & Tsou's, 2001, study and Kennedy et al.'s, 2009, studies), it created a situation in which participants' attention would have to be divided between the target and the cursor, in order to perform the task. This should provide a natural form of terminal exposure, as participants switch from attending to the target back to attending to their expected cursor position.

Perceptual Adaptation Without Compensation for the Misalignment

Miall and Jackson (2006) found no behavioural adaptation to a 300 ms delay over the course of a 30 minute session, in contrast to results found with predictable targets (as in Cunningham et al., 2001, and Kennedy et al.'s, 2009, results). That they also found behavioural aftereffects in the absence of adaptive behaviour would, they argued, contradict earlier research (e.g. Redding & Wallace, 1993) showing that aftereffects develop after adaptive behaviour, also noting that their results showed adaptive behaviour developing much more slowly than in Cunningham et al.'s (2001) experiments. They argued instead that the supposed behavioural aftereffects in their study could be explained as the transfer of a strategy of slowed responses from the exposure trials to the catch trials.

However, there is an alternative explanation. Miall and Jackson's (2006) apparent aftereffects could be accounted for by rapid adaptation (in line with Cunningham, Billock, & Tsou, 2001, and Stetson et al., 2006, and also in line with the established time-course of adaptation to spatial misalignment, Redding et al., 2005) during the first session of the first day, and the initial lack of performance improvement despite adaptation could be explained by the unpredictability of the target. The slowly developing performance improvement thereafter could be due to a gradual acquisition of skills, in more precise joystick handling and in predicting the trajectory of the target.

The idea that adaptation could occur without being accompanied by performance improvement seems paradoxical, if one does not consider Bedford's distinction between perceptual and world learning. There is every opportunity for perceptual learning in Miall and Jackson's (2006) exposure task: consistently, the visual feedback of a participant's joystick movements corresponds to the actual position of the joystick 300 milliseconds in the past. Assuming the participants perceive the cursor to be visual feedback of their actions, this apparent error in interpreting sensory information - since no object can be in two places at once - could motivate perceptual change.

But whether we could learn to act with the delay as once we acted without it is another matter entirely. The non-zero duration of actions in the world, combined with the delays imposed by neural transmission, mean that we are always living (perceiving and acting) in the past. To maintain a given level of accuracy in our interactions with the world, we must predict further into our future (i.e. the present) the further into the past we are living. Whether adaptation is effected through world learning or perceptual learning, or a combination of the two, the fact remains that - if visual information about a target's movements becomes available 300 milliseconds later than it used to, and if that target is not perfectly predictable over a 300 millisecond timescale - we will never regain normal accuracy in tracking it. Thus, except in entirely predictable tasks, we should not expect complete compensation (or, necessarily, any compensation) for increased delays in temporal adaptation, as measured by performance error, whatever the means by which the adaptation is effected.

Direct Effects of Temporal Misalignment

Nonetheless, some aspects of performance error may be reduced, even with relatively unpredictable targets. The immediate impact of an increase in, say, motor delay would be to make any action late by that amount. If no compensation of any sort occurred, one would expect actions to remain consistently lagged behind their intended timing by the same amount. Prior to any compensation, one would also expect overshoots. If a participant attempted to accelerate forward but, because of the delay, saw no consequences of that attempt, they could continue to accelerate, thus overshooting their intended speed or position. Any subsequent correction would be subject to the same overshoot. Thus, one would expect direct effects in two ways: an increase in the temporal lag of actions behind their target, and an increase in variable spatial error around that lagged trajectory. In the obstacle avoidance task used in Chapter 1, any form of increased error could equally be responsible for any change in the frequency of obstacle-crashes. In the task used in Chapter 2, the restricted range of movement available would have meant that overshoot of the target location was impossible.

Increased Precision as an Adaptive Response

If perceptual adaptation brought no performance improvement with it, it would seem odd to attempt it. However, although it may be impossible to compensate directly for a temporal delay in a sufficiently unpredictable task, there may be other adaptive changes in behaviour that compensate for the delay indirectly. In addition to the direct impact of increased visuomotor delay on the lag of the motor system behind any visual target, such an asynchrony may also affect online control and corrections. If a motor command is executed and visual feedback does not immediately reflect it, this may motivate motor commands in the same direction, resulting in an overshoot and subsequent overcompensation. Thus, a visuomotor delay should, in a relatively unpredictable coordination task, not only make motor actions lag behind a visual target (constant error; inaccuracy), but should also increase the imprecision of the motor actions (variable error; imprecision). If the delayed visual feedback were perceptually bound to the motor action, such that the expected time of visual feedback corresponded to the observed time, one would expect such overshooting and imprecision to be reduced, even if the temporal lag could not be compensated for directly. Thus, in the present research, I assessed both temporal inaccuracy (the lag of motor actions behind a target trajectory) and spatial imprecision (the root mean square spatial error between motor actions and a target trajectory, after adjusting for the lag).

I sought first to replicate Miall and Jackson's study but with the addition of perceptual measures. However, 300 ms is a large delay relative to developmental and environmental variations in neural processing time, as noted in Chapter 2, and for intersensory misalignment smaller delays (100 ms) have produced more perceptual adaptation (Stetson et al., 2006). Thus, I also included a 100 ms delay condition.

Experiment 3.0

Method

Participants. Thirty-six participants were recruited from the paid participant panel at Cardiff University, and were each paid £10. The participants were randomly assigned to each of the three conditions.

Display. The display consisted of a centred pale blue cross-hair, a green circle (the target) and a white square (the cursor). During each trial, the target followed a trajectory defined, in each axis, as the sum of five inharmonic sinusoids (with frequencies of 0.06, 0.11, 0.13, 0.25 and 0.33 Hz) with phases randomized independently for each trial, multiplied by a half cosine to ensure that it started and finished at the centre of the display. The participant controlled the cursor position with the joystick.

Design. A three level, between-participants design was used. The independent variable was delay (0 ms | 100 ms | 300 ms). The procedure consisted of five consecutive phases (pre-training | base-line | pre-test | exposure | post-test).

Base-line procedure. The base-line phase consisted of 10 trials of the tracking task, with immediate visual feedback.

Exposure procedure. The exposure phase consisted of three blocks of 27 trials of the tracking task, with interleaved rest periods. After every sixth trial during exposure, there was a 20 second rest period; and, after each block, there was a two minute rest period.

In each trial, which lasted for 20 seconds, participants attempted to track a moving target by controlling a cursor with a joystick. In the baseline trials, the cursor's position depended on the current position of the joystick; during exposure trials, the cursor position was determined by group assignment as follows: For the control group, it was still slaved to the current joystick position, whereas for the 100ms and 300ms conditions, it depended on the position of the joystick 100 ms or 300 ms in the past.

Feedback was varied between participants, with one group receiving immediate visual feedback (control), one receiving 100 ms delayed feedback (100 ms), and one receiving 300 ms delayed feedback (300 ms).

Pre-test and post-test procedure. In both the pre-test and the post-test phase, the staircase method was used to determine the point of subjective equality in temporal order judgments between the onset of a brief visual stimulus and the termination of a one second joystick movement. As in Experiment 2.2, two interleaved staircases were used, with one starting at a +200 asynchrony, and the other starting at a -200 asynchrony. The step size was 100 ms (although, because of the variable nature of participants' motor actions, the psychometric function was sampled with a finer grain than that would imply) and each staircase terminated after 10 reversals.

For each trial of the temporal order judgment task, participants saw an arrow on the screen - randomly pointing left or right - then heard a beep, which was the cue for them to start making a joystick movement from the central position of the joystick to the furthest position in the direction of the arrow, to reach the furthest point one second after the beep. A grey square was briefly presented at the centre of the screen at a time between 100 ms and 1900 ms after the beep, selected by the staircase method. Participants were then presented with the question "Which was first...? joystick or flash" on the screen. They had been told to press the left button on the joystick if they believed that they had reached the furthest point on the joystick before the flash appeared, and to press the right button if they believed the flash had appeared before they reached the furthest point on the joystick. This procedure was essentially identical to that used in Experiment 2.2 except that the question was presented in writing on a computer screen, rather than through auditory prompts.

Pre-training. During pre-training, participants were trained to produce joystick movements of one second duration in preparation for the pre-test and post-test procedure. As in the pre-test and post-test procedure, they saw an arrow pointing left or right, and heard a beep. A grey square flashed up exactly one second after the beep, and participants were told to start moving the joystick immediately after the beep and reach the end point simultaneously with the flash. When they had been accurate such that the mean absolute error for the past five trials was less than 200 ms, pre-training was completed.

Measures. For each participant were obtained two measures of the direct effects of misalignment: the mean temporal inaccuracy in the first trial (the lag of the cursor behind the target for which the spatial imprecision was minimized when the lag was reversed), and the mean spatial imprecision (the root mean square spatial error between the cursor and target, after the temporal inaccuracy was adjusted for). The temporal inaccuracy measure for each trial was obtained by finding the best fit temporal offset between the cursor and target trajectories, that is, the offset that would minimize the root mean square spatial error between the two trajectories. A more positive value indicated the cursor lagging further behind the target. The spatial imprecision measure was the root mean square spatial error between the cursor and target for that best fit temporal offset.

There were also two measures of error reduction, derived from the direct effects measures: the slope of temporal inaccuracy in a regression in terms of trial, and the slope of spatial imprecision in terms of trial. Finally for the behavioural measures, there were two measures of the incompleteness of the adaptation: the remaining temporal inaccuracy in the last trial, and the remaining spatial imprecision in the last trial. To assess perceptual adaptation, the point of subjective simultaneity (PSS) was taken by calculating the parameters of a probit regression of response in terms of observed visual lag, and the post-test PSS minus the pre-test PSS was taken as the shift in PSS. Because the imposed visuomotor misalignment was to delay the visual consequences of motor actions, the adaptive response is to perceive visual events that lag behind motor actions as being simultaneous. Thus, a more positive PSS in the post-test (visual events are objectively later when perceived to be simultaneous) would be adaptive.

For each of the behavioural measures of slope, negative numbers indicate error reduction, and for each of the remaining behavioural measures negative numbers indicate less error. Thus, the pattern of results consistent with complete adaptation to a direct effect of misalignment would be significant error reduction, and no significant difference from complete. The pattern of results consistent with partial adaptation would be the same, but with a significant difference from complete. The predicted adaptive shift was for the PSS to become more positive in the post-test, following exposure to delayed visual feedback.

Results

In both the 300 ms and the 100 ms condition, the asynchrony initially caused participants to lag behind the target, and increase their variable error around that lagged trajectory, relative to controls (marginally non-significantly so in the 100 ms condition). Neither delay group showed any performance improvement, in either temporal inaccuracy or spatial imprecision, and the effects of asynchrony detected in the first trial remained in the final trial. Thus, the results were consistent with no adaptation occurring in either group.

For each of six dependent variables (the mean of the first trial, the mean of the last trial, and the slope; of temporal inaccuracy and spatial imprecision), an ANOVA in terms of asynchrony was conducted, using Dunnett's t test to compare each of the two delay groups to the control group.

Direct effects. There was a direct effect of asynchrony on temporal inaccuracy in the first trial, $F(2,33) = 40.23$, $p < .001$, $\eta_p^2 = .71$. Participants lagged 79 ms ($SE = 31$ ms) behind controls in the 100 ms delay condition (t (22) = 2.40, $p = .03$), and 268 ms ($SE = 31$ ms) behind the controls in the 300 ms delay condition (t (22) = 8.83, $p < .001$) (See Figure 3.0). There was also an effect on spatial imprecision in the first trial, $F(2,32) = 37.42$, $p < .001$, $\eta_p^2 = .70$. This was due to greater imprecision (8.2 pixels, $SE = 1.1$ pixels) in the 300 ms delay condition than in the control condition. These groups had unequal variances (Levene's F (1,21) = 12.25, $p = .002$), so Dunnett's T3 was used for this contrast (t (21) = 7.01, $p < .001$). The 100 ms group was nonsignificantly more imprecise

(1.3 pixels, *SE* = 1.0 pixels) in the first trial ($t(21) = 2.12$, $p = .36$) (See Figure 3.1).

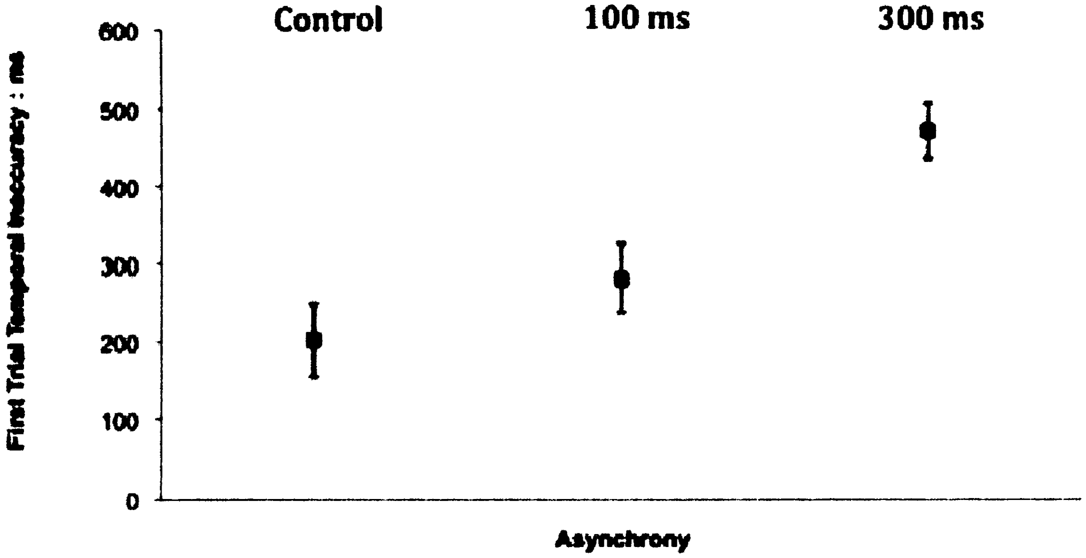

Figure 3.0. The mean lag of the cursor (controlled by joystick movement) behind the target during the first trial of exposure in Experiment 3.0, for each asynchrony group. Error bars are 95% confidence intervals. More positive values indicate that the participant-controlled cursor lagged further behind the target during the first trial.

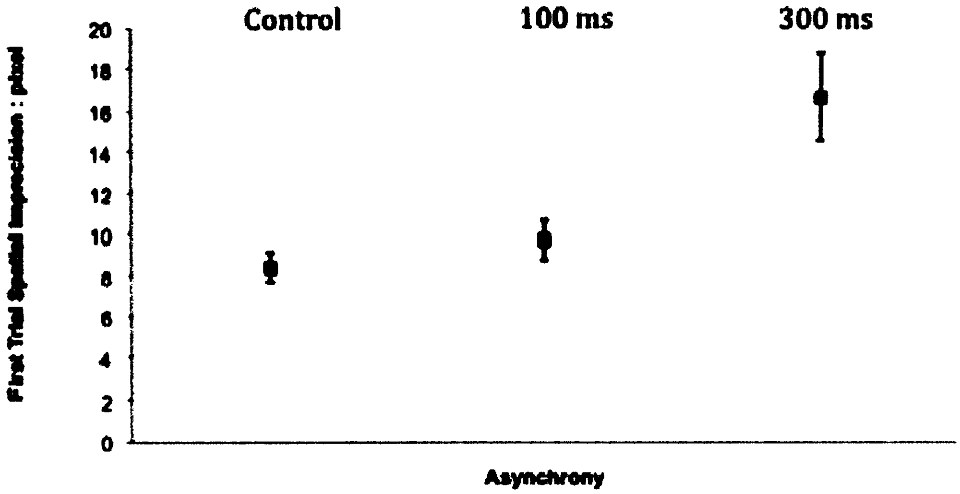

Figure 3.1. The mean root mean square spatial error – after adjusting for temporal inaccuracy - of the cursor (controlled by joystick movement) relative to the target during the first trial of exposure in Experiment 3.0, for each asynchrony group. Error bars are 95% confidence intervals. Larger values indicate greater variable error (greater imprecision) of the participant-controlled cursor's distance from the target, in the first trial, after taking into account its temporal lag behind the target.

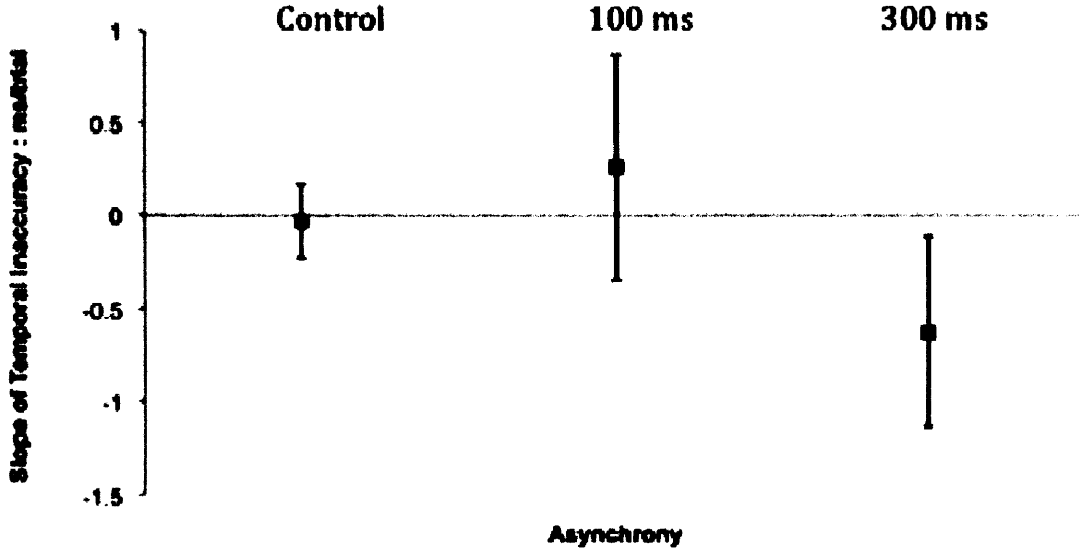

Figure 3.2. The mean rate of change of lag of the cursor behind the target, obtained from a regression of temporal inaccuracy in terms of trial number in Experiment 3.0, for each asynchrony group. Error bars are 95% confidence intervals. More negative values indicate more adaptive reduction in temporal inaccuracy over the course of exposure.

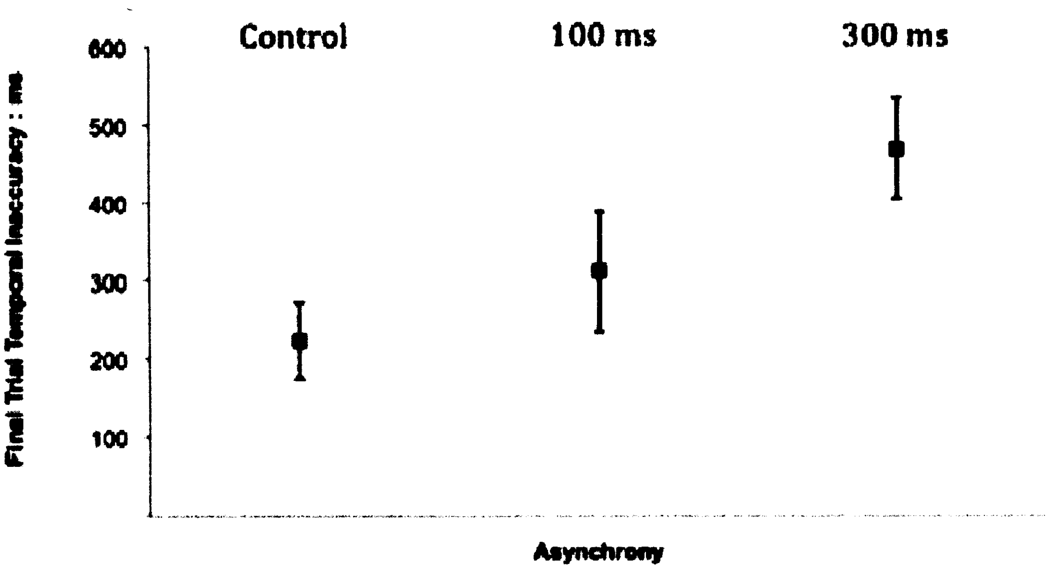

Figure 3.3. The mean lag of the cursor (controlled by joystick movement) behind the target during the final trial of exposure in Experiment 3.0, for each asynchrony group. Error bars are 95% confidence intervals. More positive values indicate greater lag of the participant-controlled cursor's distance behind the target, in the final trial.

Adaptation. The rate of change of temporal inaccuracy was affected by asynchrony, $F(2,32) = 3.47, p = .04, \eta_p^2 = .18$. Both control-delay comparisons had unequal variances (Levene's F (1,22) = 6.51, $p = .02$ for the 100 ms group, and Levene's F (1,21) = 6.54, $p = .02$ for the 300 ms group), so Dunnett's T3 was used. There was no significant difference between the control and the 100 ms delay group ($t(22) = 0.91, p = .74$) or between the control and the 300 ms delay group ($t(21) = 2.19, p = .15$) (See Figure 3.2). There was an effect of asynchrony on temporal inaccuracy in the final trial, $F(2,31) = 13.40, p < .001, \eta_p^2 = .46$. Participants fell 88 ms (*SE* = 45 ms) short of complete adaptation in the 100 ms delay condition (t (22) = 1.89, $p = .11$), and 244 ms (*SE* = 47 ms) short of complete adaptation in the 300 ms delay condition (t (22) = 6.04, $p < .001$) (See Figure 3.3).

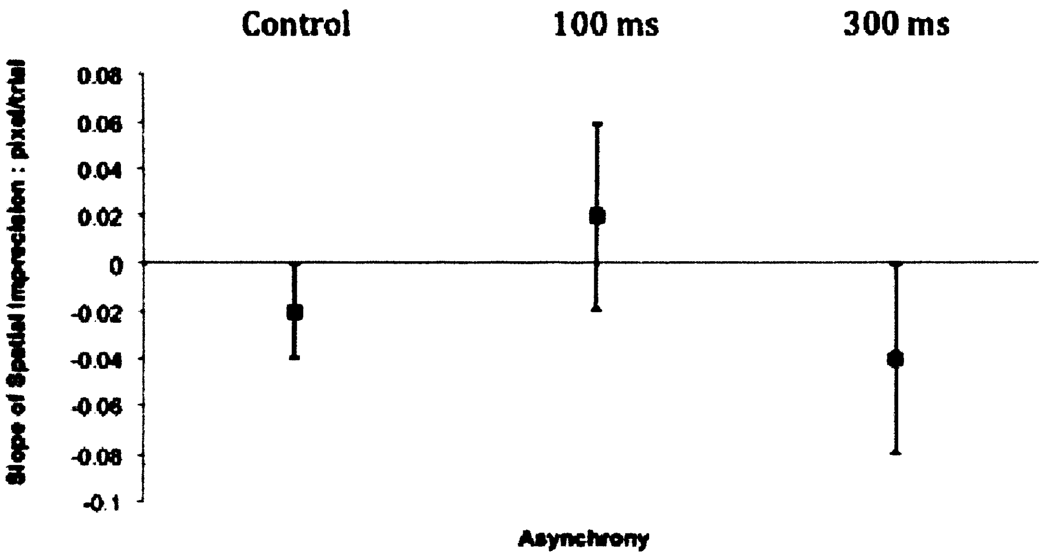

Figure 3.4. The mean rate of change of spatial imprecision (after adjusting for temporal inaccuracy), obtained from a regression of spatial imprecision in terms of trial number in Experiment 3.0, for each asynchrony group. Error bars are 95% confidence intervals. More negative values indicate more adaptive reduction in spatial imprecision over the course of exposure.

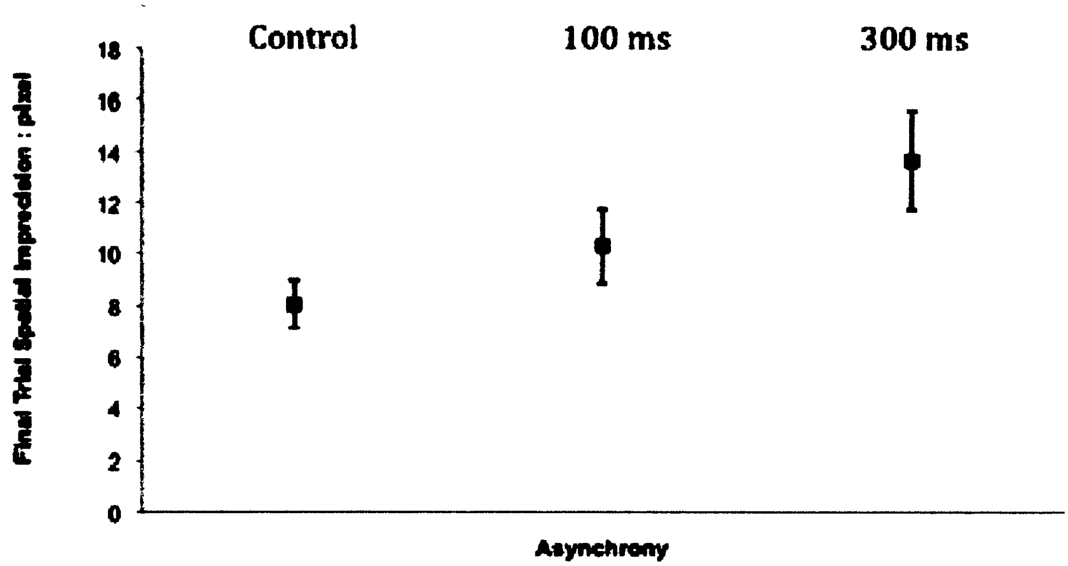

Figure 3.5. The mean root mean square spatial error – after adjusting for temporal inaccuracy - of the cursor (controlled by joystick movement) relative to the target during the final trial of exposure of Experiment 3.0, for each asynchrony group. Error bars are 95% confidence intervals. Larger values indicate greater variable error (greater imprecision) of the participant-controlled cursor's distance from the target, in the final trial, after taking into account its temporal lag behind the target.

The rate of change of spatial imprecision was not affected by asynchrony, $F(2,31) = 0.31, p = .74, \eta_p^2 = .02$ (See Figure 3.4). In the final trial, the effect of asynchrony on imprecision remained, $F(2,31) = 14.27, p < .001, \eta_p^2 = .48$. This was due to greater imprecision (5.6 pixels, $SE = 1.1$ pixels) in the 300 ms delay condition than in the control condition. These groups had unequal variances (Levene's $F(1,20) = 5.30, p = .03$), so Dunnett's T3 was used for this contrast ($t(20) = 5.42, p = .001$). The 100 ms group was marginally nonsignificantly more imprecise (1.3 pixels, *SE* = 1.0 pixels) in the final trial (t (22) = 2.59, $p = .05$) than the control group (See Figure 3.5).

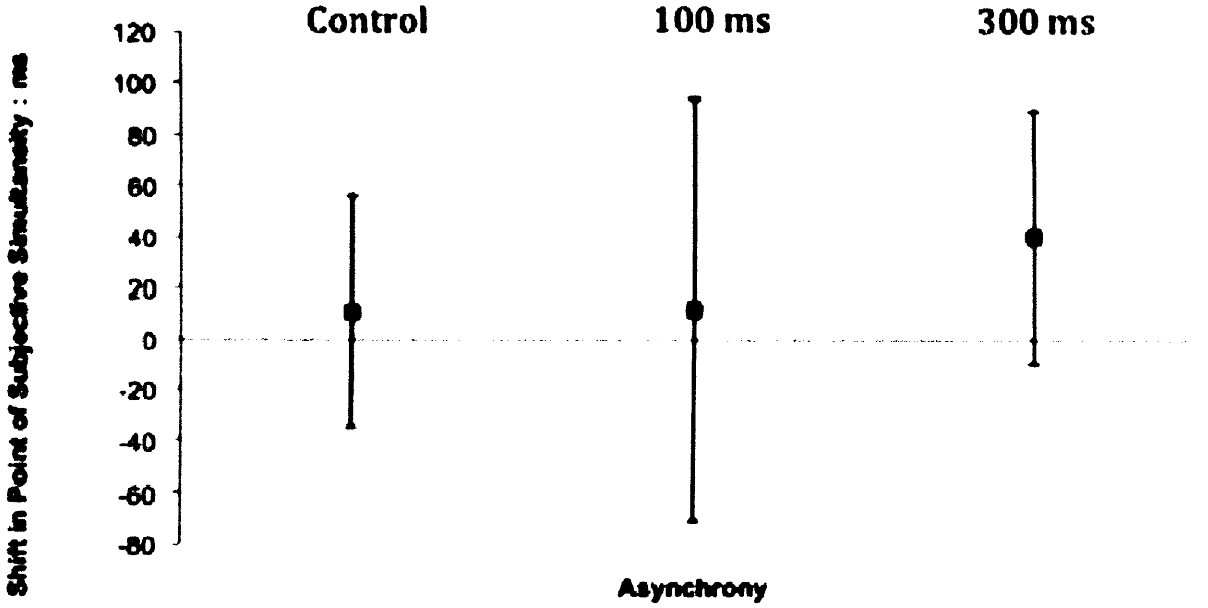

Figure 3.6. The mean point of subjective visuomotor synchrony, obtained from a probit regression in Experiment 3.0, for each asynchrony group. More positive numbers indicate that visual events had to be objectively later in order to be judged simultaneous; this being the direction of shift which would be adaptive in response to objective delayed visual feedback. Error bars are 95% confidence intervals.

Perceptual adaptation. There was no effect of asynchrony on shift in perceived visuomotor simultaneity, $F(2,31) = 0.27$, $p = .77$, $\eta_p^2 = .02$ (See Figure 3.6).

Discussion

Participants showed no behavioural or perceptual adaptation to the visuomotor misalignment in Experiment 3.0. Given the relatively unpredictable nature of the target trajectory, there may be little motivation to improve performance. With pointing towards a visual target, a range of errors centred on perfect performance is possible; thus if one is consistently off to one side, one knows one is going wrong. Similarly, in a predictable temporal task such as the head rotation task used in Chapter 2, accurate performance (with variation around it) is clearly achievable. In contrast, this is a task in which accurate performance may be unattainable, and in practice participants vary around an positive lag behind the target. Thus, in Experiment 3.1 three new measures were introduced to address this problem. More predictable trajectories were used, graded between the complexity of Experiment 3.0's exposure task and the simplicity of Chapter 2's exposure task. Participants were given performance feedback in the form of a bar at the top of the screen, which moved to the left or right, depending on performance (calculated based on the ratio of time spent in the proximity of the target to time spent away from it), relative to their own recent performance. This was to ensure that, despite the differences in difficulty across the three predictability conditions, participants in each group should be motivated to improve their performance. Finally, in Experiment 3.1, the trajectory was, for each participant, held constant across all trials, while remaining randomized across participants. Each of these measures were expected to facilitate adaptation.

Experiment 3.1

Method

Sixty participants were recruited from the undergraduate participant panel at Cardiff University, in part fulfillment of their course requirements. The participants were randomly assigned to each of the six conditions.

Design. A 2x3 between-participants design was used. The independent variables were delay (0 ms | 100 ms) and predictability (predictable | semipredictable | unpredictable). The procedure consisted of three consecutive phases (pre-test | exposure | post-test).

Display, and exposure procedure. For the 'unpredictable' conditions, the display and procedure was the same as in Experiment 3.0, except that the exposure phases consisted of 96 trials of 10 seconds each, with no rest periods. The remaining predictability conditions used different trajectories: In the 'semipredictable' conditions a one-dimensional trajectory was formed from the sum of two inharmonic sinusoids (frequencies: 0.4 and 1 Hz) of randomized phase, and in the 'predictable' conditions, a single 1 Hz one-dimensional sinusoid was used (comparable to the simple back and forth movements required in Chapter 2's head rotation exposure task).

Pre-test and post-test procedure. The procedures were similar to Experiment 3.0's, except that the motor action used was a half-sinusoid, from a centred position to the side indicated by the arrow and back to centre, in one flowing movement, and the visual event was an equivalent movement of a white square on the screen, moving from centred to the side and back again in a half-sinusoid. Rather than training participants to make movements at a certain time, they were asked to make the movement at any point between two beeps, and the visual stimulus was placed relative to the mean timing of the movement in the most recent five trials.

Results

With the unpredictable trajectory (the one used in Experiment 3.0), participants in the 100 ms condition (relative to controls) initially lagged behind the target and showed increased variable error, and there was a marginally nonsignificant reduction in temporal inaccuracy, leading to a final trial in which adaptation was not significantly different from complete as regards temporal inaccuracy or spatial imprecision.

In contrast, no direct effects on temporal inaccuracy were noted in the first trials of the semipredictable and predictable 100 ms delay conditions, relative to controls. This suggests very rapid compensation for the delay when dealing with more predictable trajectories. Curiously, in the final trial of the semipredictable trajectory condition, the 100 ms group had developed a significant lag behind the target, relative to controls. There were direct effects on spatial imprecision in the first trial of the semipredictable condition, and in the last trial of the predictable condition, with no significant adaptation for this measure in either condition. None of the three predictability conditions showed an effect of asynchrony on the relative perceived timing of visual and motor events.

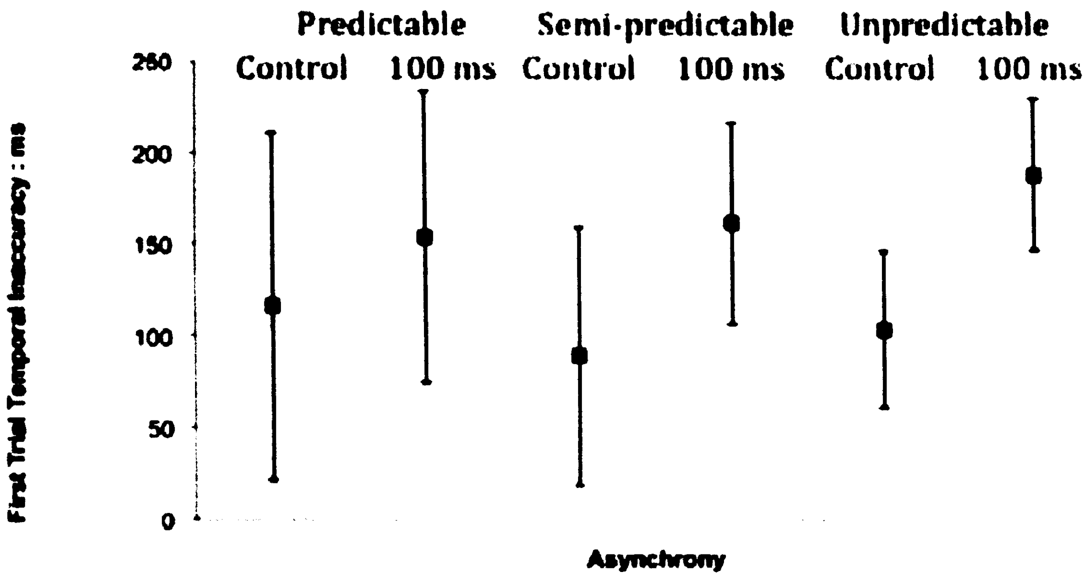

Figure 3.7. The mean lag of the cursor (controlled by joystick movement) behind the target during the first trial of exposure in Experiment 3.1, for each predictability and asynchrony group. Error bars are 95% confidence intervals. More positive values indicate that the participant-controlled cursor lagged further behind the target during the first trial.

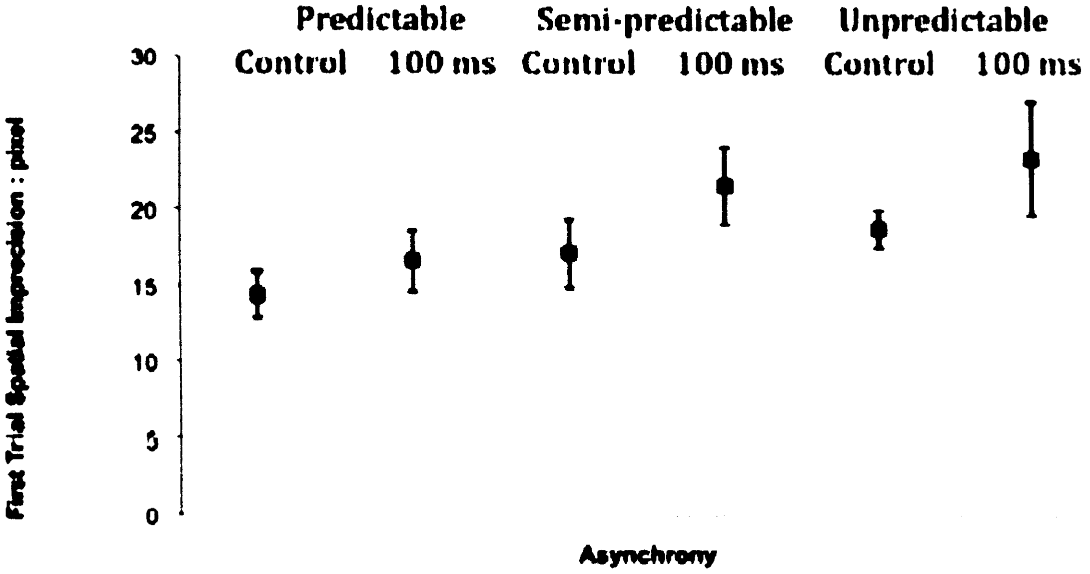

Figure 3.8. The mean root mean square spatial error – after adjusting for temporal inaccuracy - of the cursor (controlled by joystick movement) relative to the target during the first trial of exposure in Experiment 3.1, for each predictability and asynchrony group. Error bars are 95% confidence intervals. Larger values indicate greater variable error (greater imprecision) of the participant-controlled cursor's distance from the target, in the first trial, after taking into account its temporal lag behind the target.

Direct effects. With the predictable trajectory, there was no direct effect of asynchrony on temporal inaccuracy in the first trial, $F(1,18) = 0.35$, $p = .56$, $\eta_p^2 = .02$. Participants lagged 37 ms (*SE* = 63 ms) behind controls in the 100 ms delay condition (See Figure 3.7). There was also no significant effect of asynchrony on spatial imprecision in the first trial, $F(1,18) = 2.97$, $p = .10$, $\eta_p^2 = .14$ (See Figure 3.8).

With the semi-predictable trajectory, there was also no direct effect of asynchrony on temporal inaccuracy in the first trial, $F(1,18) = 2.53$, $p = .13$, $\eta_p^2 =$

.12. Participants lagged 72 ms (*SE* = 46 ms) behind controls in the 100 ms delay condition. There was, however, a significant effect on spatial imprecision, such that participants in the 100 ms delay condition were more imprecise (4.5 pixels, *SE* = 1.7 pixels) than in the control condition, $F(1,18) = 6.74$, $p = .02$, $\eta_p^2 = .28$.

With the unpredictable trajectory, there was a direct effect of asynchrony on temporal inaccuracy in the first trial, $F(1,17) = 7.80$, $p = .01$, $\eta_p^2 = .31$. Participants lagged 85 ms (*SE* = 30 ms) behind controls in the 100 ms delay condition. There was also an effect on spatial imprecision, such that participants in the 100 ms delay condition were more imprecise (4.6 pixels, *SE* = 2.0 pixels) than in the control condition, $F(1,18) = 5.35$, $p = .03$, $\eta_p^2 = .23$.

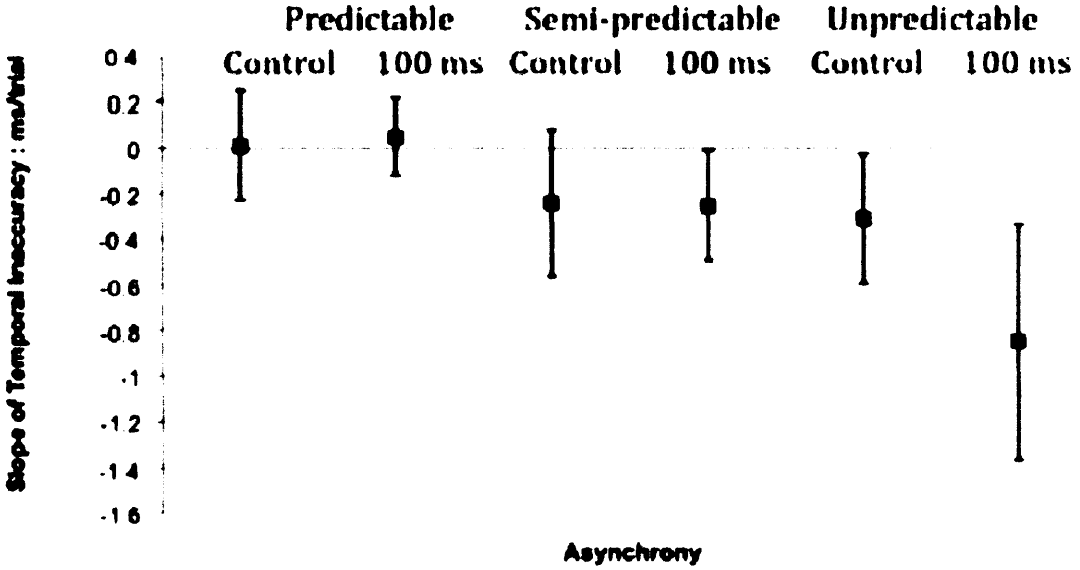

Figure 3.9. The mean rate of change of lag of the cursor behind the target, obtained from a regression of temporal inaccuracy in terms of trial number in Experiment 3.1, for each predictability and asynchrony group. More negative values indicate more adaptive reduction in temporal inaccuracy over the course of exposure.

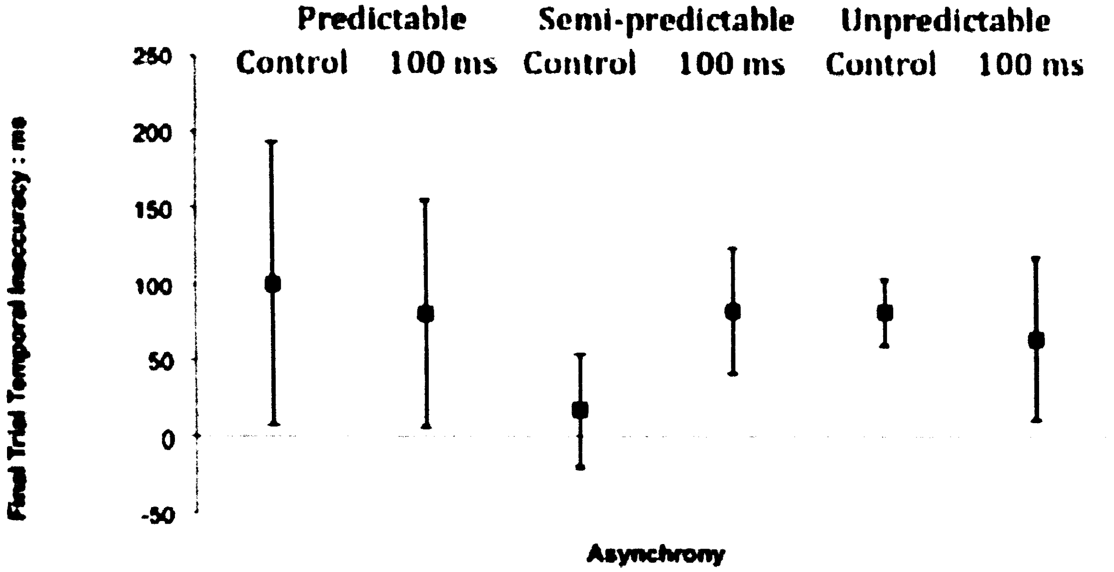

Figure 3.10. The mean lag of the cursor (controlled by joystick movement) behind the target during the final trial of exposure in Experiment 3.1, for each predictability and asynchrony group. Error bars are 95% confidence intervals. More positive values indicate greater lag of the participant-controlled cursor's distance behind the target, in the final trial.

Adaptation. With the predictable trajectory, there was no effect of asynchrony on the rate of change of temporal inaccuracy, $F(1,18) = 0.07, p = .80, \eta_p^2 < .01$. Participants showed nonsignificantly more error reduction (0.01 ms/trial, *SE* = 0.20 ms/trial) than controls in the 100 ms delay condition (See Figure 3.9). In the final trial temporal inaccuracy was not different across conditions, $F(1,18) = 0.11, p = .75, \eta_p^2 < .01$ (See Figure 3.10). The rate of change of spatial imprecision was also not affected by asynchrony, $F(1,17) = 0.02, p = .90, \eta_p^2 < .01$ (See Figure 3.11). In the final trial, an effect of asynchrony on imprecision had developed, $F(1,17) = 9.32, p = .007, \eta_p^2 < .35$, such that participants in the 100 ms delay condition were more imprecise (2.3 pixels, *SE* = 0.7 pixels) than in the control condition (See Figure 3.12).

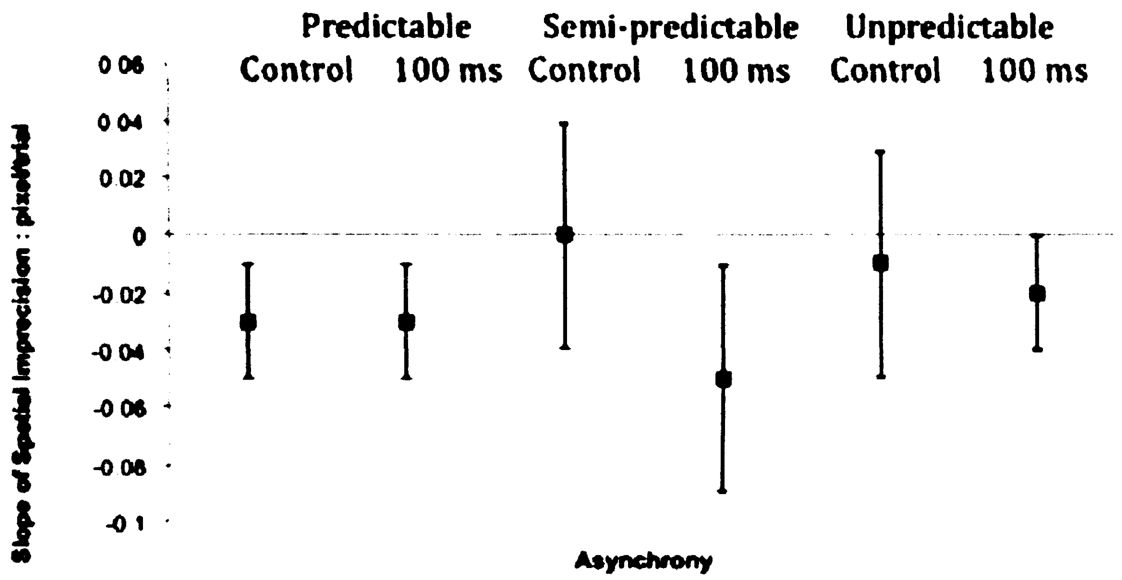

Figure 3.11. The mean rate of change of spatial imprecision (after adjusting for temporal inaccuracy), obtained from a regression of spatial imprecision in terms of trial number in Experiment 3.1, for each predictability and asynchrony group. More negative values indicate more adaptive reduction in spatial imprecision over the course of exposure.

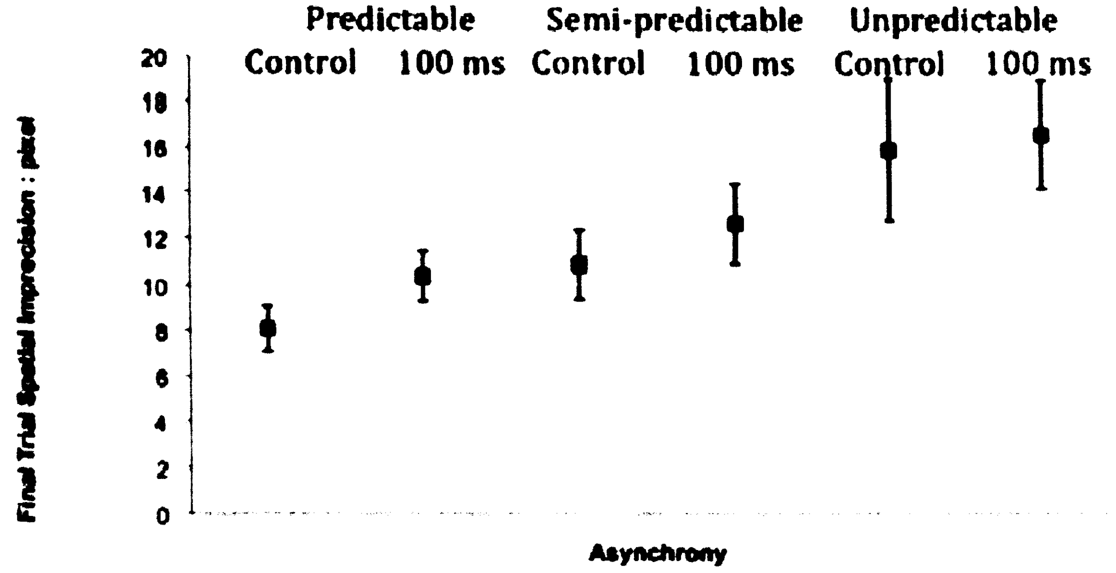

Figure 3.12. The mean root mean square spatial error – after adjusting for temporal inaccuracy - of the cursor (controlled by joystick movement) relative to the target during the final trial of exposure in Experiment 3.1, for each predictability and asynchrony group. Error bars are 95% confidence intervals. Larger values indicate greater variable error (greater imprecision) of the participant-controlled cursor's distance from the target, in the final trial, after taking into account its temporal lag behind the target.

With the semi-predictable trajectory, there was no effect of asynchrony on the rate of change of temporal inaccuracy, $F(1,16) < 0.01$, $p = .95$, $\eta_p^2 < .01$. Participants showed nonsignificantly more error reduction (0.01 ms/trial, *SE* = 0.20 ms/trial) than controls in the 100 ms delay condition. In the final trial, the 100 ms delay group had become significantly short (65 ms, SE = 28 ms) of full compensation, $F(1,18) = 5.26$, $p = .04$, $\eta_p^2 = .24$. The rate of change of spatial imprecision was also not affected by asynchrony, $F(1,17) = 1.39$, $p = .25$, $\eta_p^2 = .08$. However, the effect of asynchrony on imprecision was no longer significant in the final trial, $F(1,16) = 2.30$, $p = .15$, Hη_p^2 p2 = .13.

With the unpredictable trajectory, there was a marginally nonsignificant effect of asynchrony on the rate of change of temporal inaccuracy, $F(1,17) = 3.04$, $p = .10$, $\eta_p^2 = .15$. Participants showed more error reduction (0.54 ms/trial, SE = 0.31 ms/trial) than controls in the 100 ms delay condition. In the final trial temporal inaccuracy was not different across conditions, $F(1,16) = 0.31$, $p = .59$, $\eta_p^2 = .02$. The rate of change of spatial imprecision was not affected by asynchrony, $F(1,18) = 0.14$, $p = .71$, $\eta_p^2 < .01$. However, the effect of asynchrony on imprecision was no longer significant in the final trial, $F(1,17) = 0.11$, $p = .75$, $\eta_p^2 < .01$.

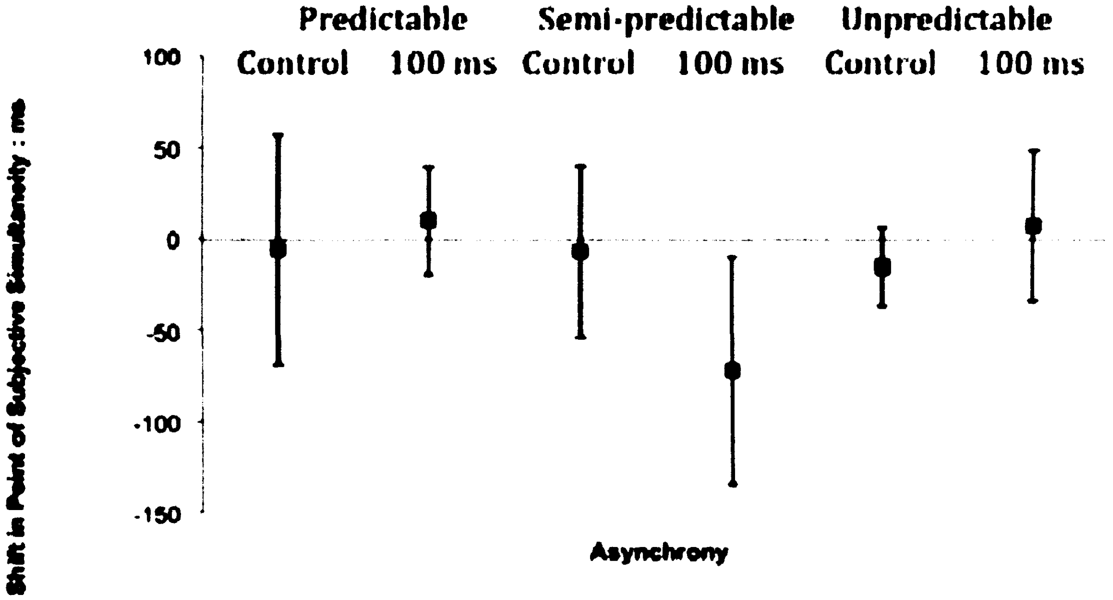

Figure 3.13. The mean point of subjective visuomotor synchrony in Experiment 3.1, obtained from a probit regression, for each predictability and asynchrony group. More positive numbers indicate that visual events had to be objectively later in order to be judged simultaneous; this being the direction of shift which would be adaptive in response to objective delayed visual feedback. Error bars are 95% confidence intervals.

Perceptual adaptation. With the predictable trajectory, there was no effect of asynchrony on shift in perceived visuomotor simultaneity, $F(1,16) = 0.17, p = .68, \eta_p^2 = .01$. With the semipredictable trajectory, there was also no effect of asynchrony on shift in perceived visuomotor simultaneity, $F(1,18) = 2.68, p = .12, \eta_p^2 = .13$. With the unpredictable trajectory, there was also no effect of asynchrony on shift in perceived visuomotor simultaneity, $F(1,17) = 0.86, p = .37, \eta_p^2 = .05$ (See Figure 3.13).

Discussion

So, with these modifications to Miall and Jackson's (2006) stimulus, some adaptation – in some cases, very rapid and complete adaptation – was observed. However, none of it appeared to have been effected by, or accompanied, by perceptual adaptation of the sort detected in spatial adaptation. Two factors may have discouraged perceptual adaptation. The lack of randomization of trajectory across trials may have made it possible for participants to learn a sequence of movements that could be shifted in phase as easily as a simple sinusoid. And, as in all the experiments thus far, the asynchrony was introduced immediately. Research from the spatial literature (e.g. Kluzik, Diedrichsen, Shadmehr, & Bastian, 2006) suggests that gradual introduction of a misalignment may produce more perceptual adaptation. Thus, in the next experiment, across-trial randomization was reintroduced, along with an additional gradual delay condition.

Experiment 3.2

Method

Sixty participants were recruited from the paid participant panel at Cardiff University, and each paid 10 pounds. The participants were randomly assigned to each of the six conditions.

A 3x2 between-participants design was used. The independent variables were delay (0 ms | immediate 100 ms | gradual 100 ms) and predictability (semipredictable | unpredictable). The procedure and display were as in Experiment 3.1. In the gradual 100 ms condition, the delay was 0 ms in the first six trials, and then increased by 100/6 ms for each subsequent block of six trials, remaining at 100 ms once it reached that value.

Results

Direct effects. With the semi-predictable trajectory, there was a direct effect of asynchrony on temporal inaccuracy in the first trial, $F(2,27) = 13.83, p < .001, \eta_p^2 = .51$. Participants lagged 167 ms ($SE = 32$ ms) behind controls in the immediate 100 ms delay condition ($t\,(18) = 5.04, p < .001$), but lagged nonsignificantly 54 ms ($SE = 34$ ms) behind controls in the gradual 100 ms delay condition ($t\,(18) = 1.58, p = .19$) (See Figure 3.14). However, there was no effect on spatial imprecision in the first trial, $F(2,26) = 0.78, p = .47, \eta_p^2 = .06$ (See Figure 3.15).

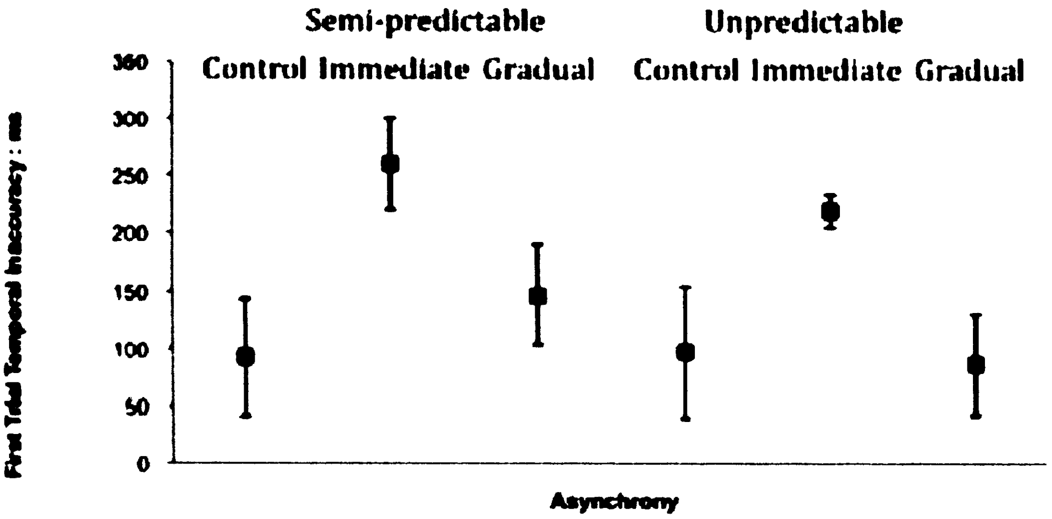

Figure 3.14. The mean lag of the cursor (controlled by joystick movement) behind the target during the first trial of exposure in Experiment 3.2, for each predictability and asynchrony group. More positive values indicate that the participant-controlled cursor lagged further behind the target during the first trial.

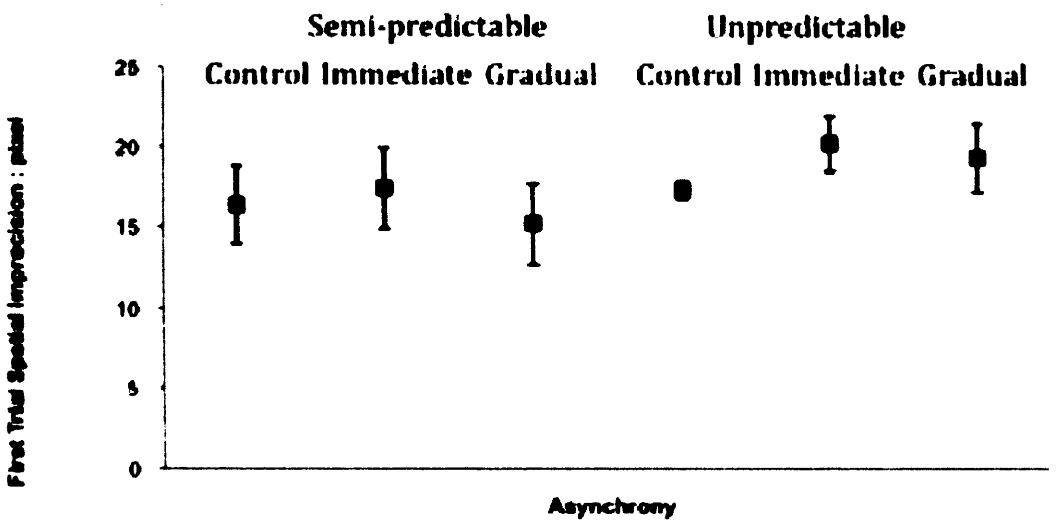

Figure 3.15. The mean root mean square spatial error – after adjusting for temporal inaccuracy - of the cursor (controlled by joystick movement) relative to the target during the first trial of exposure in Experiment 3.2, for each predictability and asynchrony group. Larger values indicate greater variable error (greater imprecision) of the participant-controlled cursor's distance from the target, in the first trial, after taking into account its temporal lag behind the target.

With the unpredictable trajectory, there was a direct effect of asynchrony on temporal inaccuracy in the first trial, *F*(2,24) = 8.11, *p* = .002, η_p^2 = .40. Participants lagged 167 ms (*SE* = 32 ms) behind controls in the immediate 100 ms delay condition. Levene's test for equality of variances indicated that these two groups did not have equal variances, *F* (1,16) = 8.07, *p* = .01, so Dunnett's T3 statistic was used to compare the group means (*t* (15) = 3.39, *p* = .004). They lagged nonsignificantly 11 ms (*SE* = 37 ms) behind controls in the gradual 100 ms delay condition (*t* (18) = 0.28, *p* = .93). There was also a marginally nonsignificant effect on spatial imprecision in the first trial, *F*(2,22) = 2.57, *p* =

.10, $\eta_p^2 = .19$. This was due to a significant difference between the immediate 100 ms delay group and the control group. Again, variances were unequal (Levene's $F(2,22) = 5.12$, $p = .04$), so Dunnett's T3 statistic was used here. The immediate 100 ms delay group were more imprecise (2.9 pixels, $SE = 0.9$ pixels) than the control group, whereas the gradual 100 ms delay group were not significantly different from controls.

Adaptation. With the semi-predictable trajectory, there was an effect of asynchrony on the rate of change of temporal inaccuracy, $F(2,25) = 6.48$, $p = .005$, $\eta_p^2 = .34$. Participants showed nonsignificantly more error reduction (0.27 ms/trial, $SE = 0.22$ ms/trial) than controls in the immediate 100 ms delay condition ($t\,(17) = 1.25$, $p = .31$). In the gradual 100 ms delay condition, however, they showed significantly more error reduction (0.27 ms/trial, $SE = 0.22$ ms/trial) than controls ($t\,(17) = 3.27$, $p = .003$) (See Figure 3.16). In the final trial, there was no effect of asynchrony on temporal inaccuracy, $F(2,25) = .30$, $p = .74$, $\eta_p^2 = .02$ (See Figure 3.17). The rate of change of spatial imprecision was marginally non-significantly affected by asynchrony, $F(2,27) = 3.05$, $p = .06$, $\eta_p^2 = .18$. Because there was unequal variance between the control and the gradual groups (Levene's $F(1,18) = 5.05$, $p = .04$), Dunnett's T3 was used to test this contrast, and showed no significant difference, $t(18) = 2.18$, $p = .14$; there was also no significance difference between controls and the immediate delay group, $t(18) = 1.40$, $p = .21$ (See Figure 3.18). The final trial showed no effect of asynchrony on spatial imprecision, $F(2,26) = 0.35$, $p = .71$, $\eta_p^2 = .03$ (See Figure 3.19).

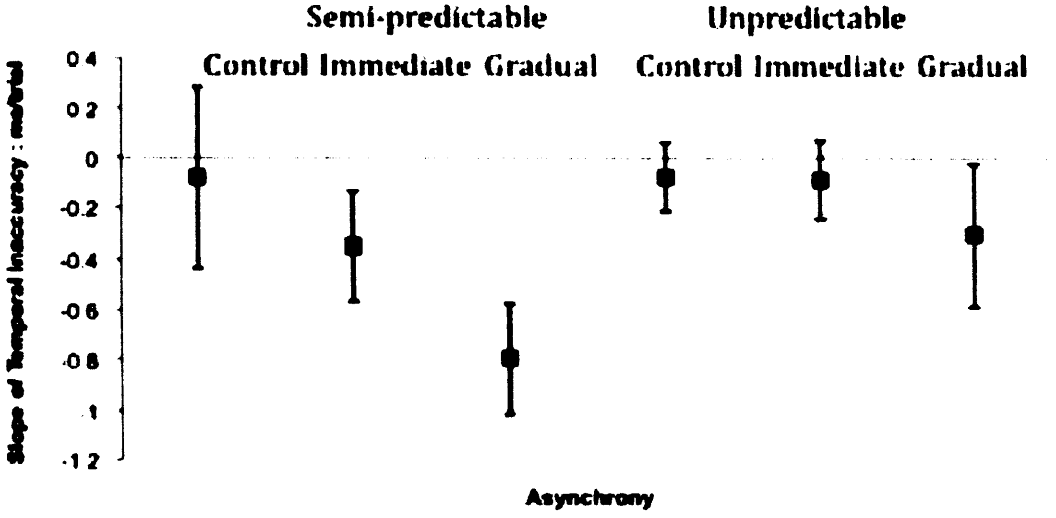

Figure 3.16. The mean rate of change of lag of the cursor behind the target in Experiment 3.2, obtained from a regression of temporal inaccuracy in terms of trial number, for each predictability and asynchrony group. More negative values indicate more adaptive reduction in temporal inaccuracy over the course of exposure.

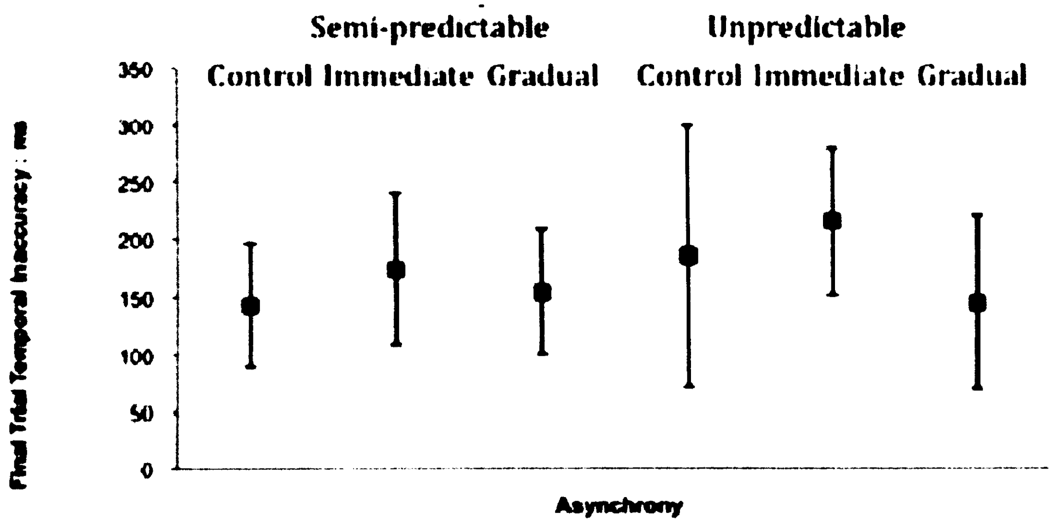

Figure 3.17. The mean lag of the cursor (controlled by joystick movement) behind the target during the final trial of exposure in Experiment 3.2, for each predictability and asynchrony group. More positive values indicate greater lag of the participant-controlled cursor behind the target, in the final trial.

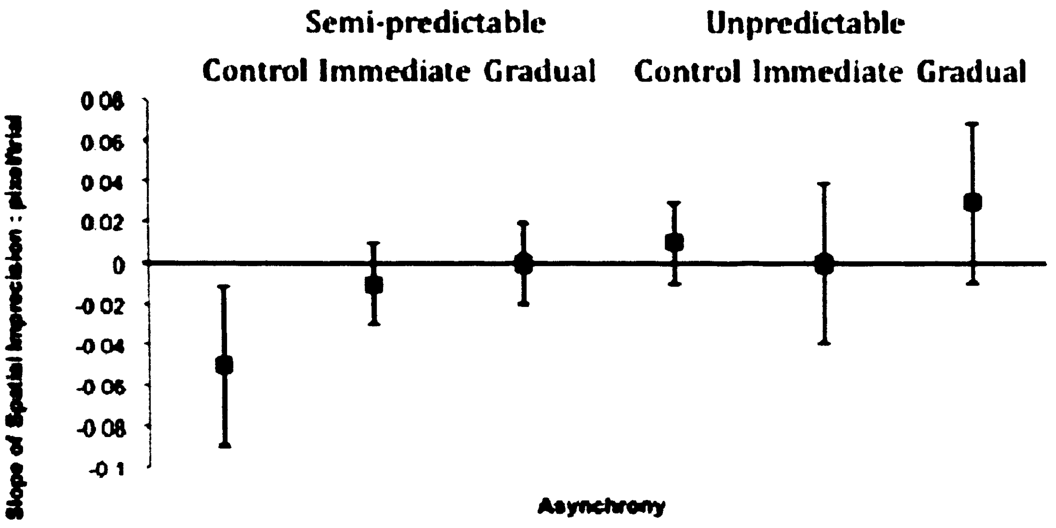

Figure 3.18. The mean rate of change of spatial imprecision (after adjusting for temporal inaccuracy) in Experiment 3.2, obtained from a regression of spatial imprecision in terms of trial number, for each predictability and asynchrony group. More negative values indicate more adaptive reduction in temporal inaccuracy over the course of exposure.

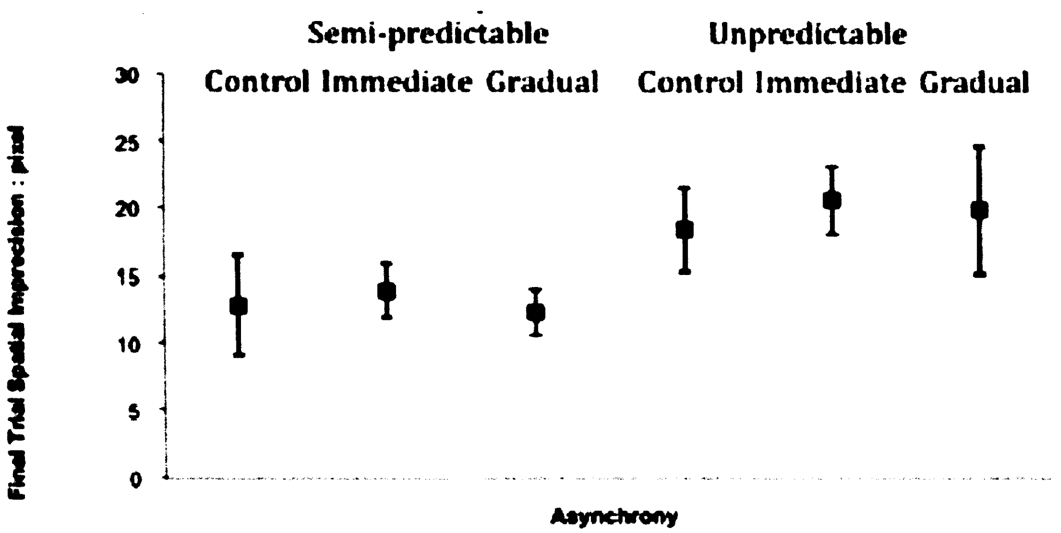

Figure 3.19. The mean root mean square spatial error – after adjusting for temporal inaccuracy - of the cursor (controlled by joystick movement) relative to the target during the final trial of exposure in Experiment 3.2, for each predictability and asynchrony group. Larger values indicate greater variable error (greater imprecision) of the participant-controlled cursor's distance from the target, in the final trial, after taking into account its temporal lag behind the target.

With the unpredictable trajectory, there was no effect of asynchrony on the rate of change of temporal inaccuracy, $F(2,25) = 1.53$, $p = .24$, $\eta_p^2 = .11$. In the final trial, there was no effect of asynchrony on temporal inaccuracy, $F(2,27) = .64$, $p = .54$, $\eta_p^2 = .05$. The rate of change of spatial imprecision was not affected by asynchrony, $F(2,25) = 1.23$, $p = .31$, $\eta_p^2 = .09$. The final trial showed no effect of asynchrony on spatial imprecision, $F(2,26) = 0.40$, $p = .67$, $\eta_p^2 = .03$.

Perceptual adaptation. With the semipredictable trajectory, there was a marginally nonsignificant effect of asynchrony on shift in perceived visuomotor simultaneity, $F(2,27) = 3.29$, $p = .05$, $\eta_p^2 = .20$. However, neither delay condition had a significant difference from the control group. The immediate 100 ms delay group was no different from the control group ($t(17) = 1.83, p = .91$). The gradual 100 ms delay group showed a marginally nonsignificant shift in the adaptive direction (52 ms, $SE = 26$ ms) relative to control ($t(18) = 1.86, p < .10$). With the unpredictable trajectory, there was no effect of asynchrony on shift in perceived visuomotor simultaneity, $F(2,25) = 0.15, p = .86, \eta_p^2 = .01$ (See Figure 3.20).

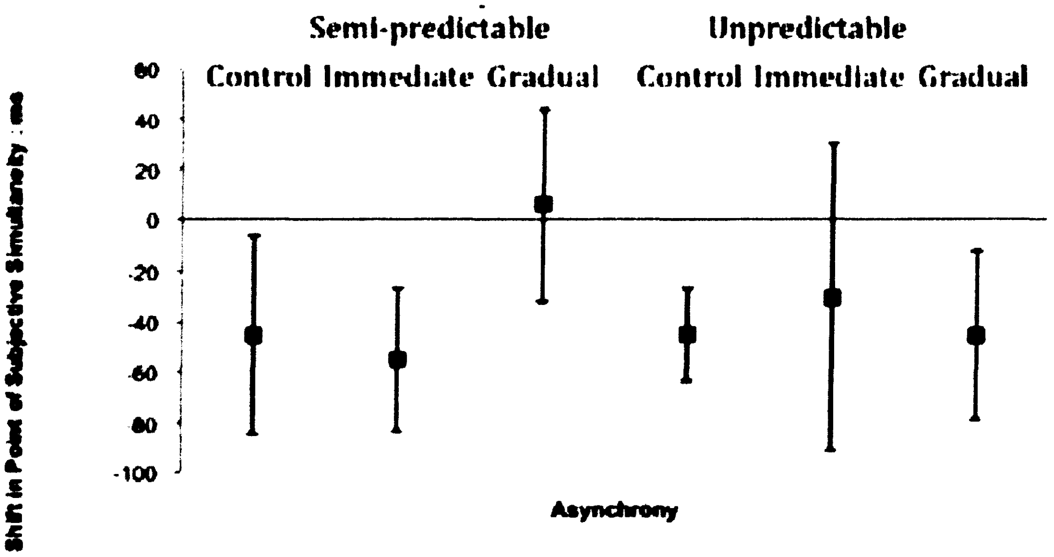

Figure 3.20. The mean point of subjective visuomotor synchrony, obtained from a probit regression, for each predictability and asynchrony group. More positive numbers indicate that visual events had to be objectively later in order to be judged simultaneous; this being the direction of aftereffect which would be adaptive in response to objective delayed visual feedback.

Discussion.

In the immediate delay conditions, both with the predictable and the semipredictable trajectories, there was an initial effect of asynchrony on the cursor's lag behind the target. Of course, in the gradual delay conditions, there was no objective difference from controls in terms of the visuomotor asynchrony, and thus the lack of effect here is expected. An initial effect on spatial imprecision was noted only in the unpredictable, immediate delay condition. Only in the semipredictable, gradual delay condition was a significant reduction in temporal error observed; however, in none of the delay conditions was the temporal inaccuracy or spatial imprecision significantly different from controls in the final trial. Only in the semipredictable, gradual delay condition was there a marginally nonsignificant shift in perceived timing of motor and visual events relative to controls.

General Discussion

In Chapter 1, my replication of Cunningham, Billock, and Tsou's (2001) predictable obstacle avoidance task did not replicate their behavioural aftereffects. In Chapter 2, behavioural but not perceptual aftereffects were demonstrated with a novel, predictable pacing task. In the present chapter, a partial replication of Miall and Jackson's (2006) unpredictable tracking task found (as did Miall & Jackson, 2006) no behavioural adaptation to a 300 ms visuomotor misalignment over the course of a 30 minute exposure phase. However, with a smaller delay (100 ms), more predictable target trajectories, and performance feedback, complete behavioural adaptation was observed over a 15 minute exposure phase.

Thus, I have shown that sufficiently small delays in visuomotor feedback can be compensated for, if a sufficiently simple and predictable target trajectory is used. However, in none of the conditions was perceptual adaptation detected by visuomotor temporal order judgments, whether or not behavioural adaptation was noted. This failure of humans to adapt perceptually to a temporal visuomotor misalignment raises many interesting questions. Perhaps assessment of the delay would require processing (for example, a crosscorrelation analysis) that might either be too complex or too slow to be of use in visuomotor coordination. Alternatively, perhaps any perceptual adaptation (however it may be effected) would not produce any behavioural advantage. Both these possibilities can be addressed through simulation modeling of perceptual adaptation in visuomotor coordination, and the first steps in that work are presented in Chapter 4.

Another option is that perceptual adaptation did occur in some or all of the exposure tasks, but that the criterion tasks were unable to detect the adaptation. Possible reasons for such a dissociation are discussed in Chapter 5; but modeling work may help to address this possibility too. Comparison of a model's behavioural performance with and without a module for perceptual adaptation may suggest behavioural measures that are sensitive to perceptual adaptation.

Chapter 4: Towards a Model of Visuomotor Adaptations to Temporal Misalignment

In the previous chapters, I presented results from a range of exposure tasks, demonstrating, in some circumstances, behavioural adaptation; but in no circumstances perceptual adaptation. This is in stark contrast to results from adaptation to spatial misalignment, and adaptation to temporal intersensory misalignment. In the present chapter I present work on a simulation model of perceptual adaptation and visuomotor coordination in a tracking task. The model provides a proof of concept that a simple, recursive estimator can respond appropriately to temporal visuomotor misalignment. Furthermore, when its estimate is used to modify percepts within the model, behavioural performance improves. However, the nature of the improvement is at odds with that found with human participants in Chapter 3, suggesting that humans take a different route to adaptation in this task.

In Chapter 3, I presented results that suggested that humans adapt to temporal misalignment by means undetectable by temporal order judgments. Interpreting such a null result is, naturally, problematic. There are two broad possibilities: either there was no perceptual involvement in the response to the misalignment, or there was perceptual involvement but the temporal order judgments were incapable of detecting it. The former would suggest that inherent differences in our relationship to time (compared with our relationship to the dimensions of space) make it either difficult or disadvantageous in some or all circumstances to adapt perceptually, whether or not a behavioural solution is available. The latter would suggest that indirect, behavioural methods would be more appropriate for assessing the type of learning that has taken place. In either case, modeling the perceptual and behavioural responses to visuomotor misalignment may help to address these questions. If models of perceptual adaptation indicate that it is behaviourally ineffective as a response to misalignment in the temporal domain, this would support the interpretation that, where behavioural solutions to temporal misalignment exist, they are preferable to any perceptual solution, and hence the absence of perceptual adaptation in any temporal visuomotor coordination paradigm. Conversely, if models of perceptual adaptation indicate that it could be effective, and further indicate behavioural consequences of perceptual adaptation, this may provide an indirect method of assessing perceptual change. Alternatively, such models could provide indications of the types of stimuli more likely to elicit perceptual adaptation responses.

Requirements of the Model

The purpose of the model (see Figure 4.0 for an outline of the model) was to test whether the addition of a perceptual adaptation process to a simple sensorimotor tracking system could result in the correct detection of misalignment and the facilitation of behavioural error reduction, in a task equivalent to those used in Experiments 3.0 to 3.2. Thus, it required a process to monitor the position of a to-be-tracked object (the target), and a process to monitor its own position (the cursor), a process to determine motor output based on the error between the target and the cursor (tracker), and – finally - a process to monitor symptoms of sensorimotor misalignment and accordingly adjust the (perceptual) input to the target and cursor monitoring processes (a perceptual adaptation module, or PAM). Burge, Ernst, and Banks (2008) had employed the Kalman filter to model adaptation to spatial visuomotor misalignment (albeit without distinguishing perceptual and behavioural components), and the present model follows Burge et al. (2008) in that respect.

Description of the Model.

Cursor Monitor

A Kalman filter was used to monitor the position and velocity of the cursor. It had as its inputs a noisy measurement of the cursor's position, and an efference copy of the last motor output from the tracker. At each time step, it projected an estimate of the current cursor position, based on its last estimate and the last motor output, compared it to the latest measurement, and combined the estimate and the measurement in a weighted average estimate of both the position and velocity. The weighting, and thus the rate of convergence, depends on the parameters of the covariance matrices of the filter (see, e.g., Burge et al., 2006). See Appendix for details of the parameters for this and the other filters.

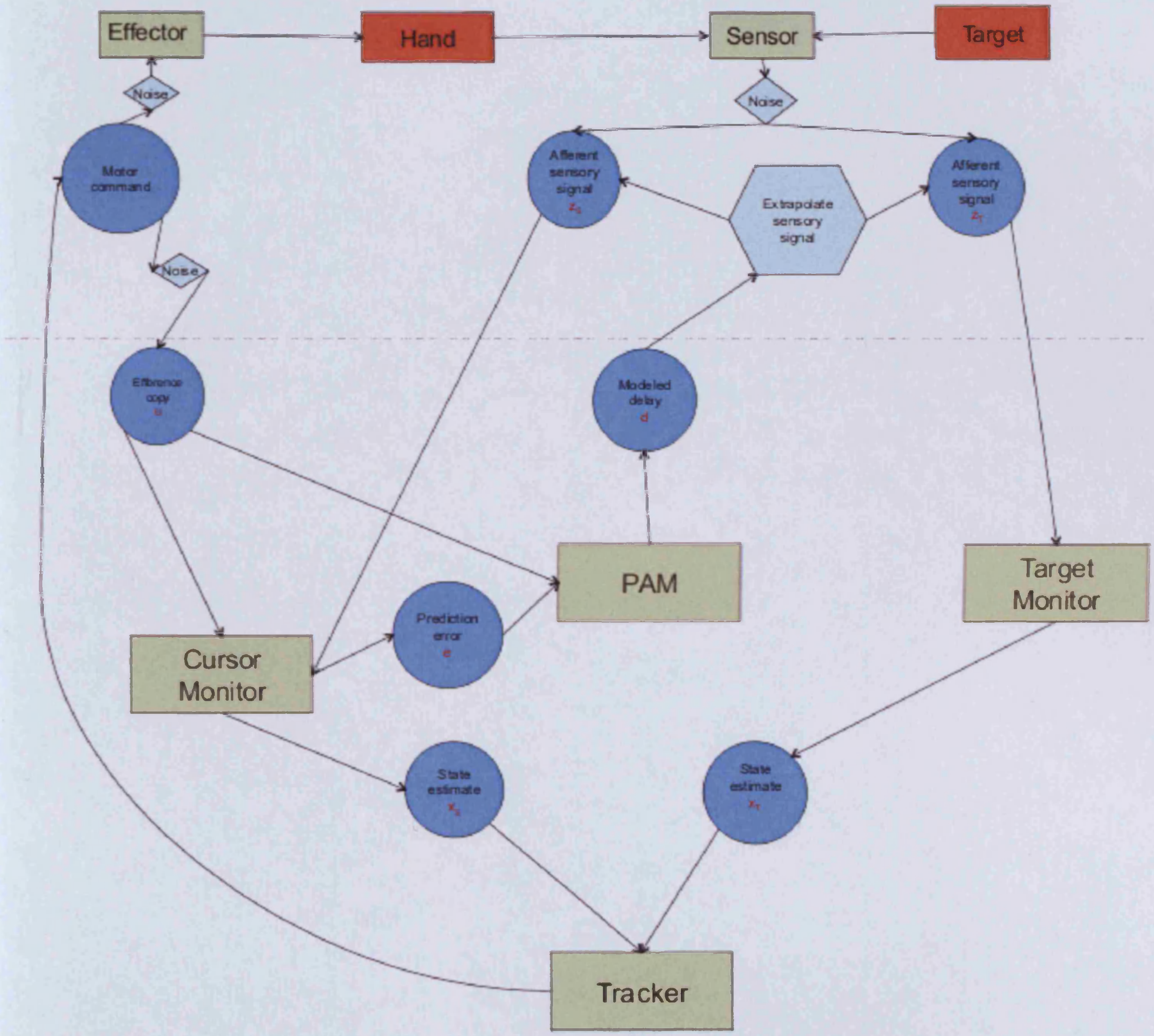

Figure 4.0 The model, showing inputs and outputs of the cursor monitor process, target monitor process, tracker and the perceptual adaptation module (PAM). Only items below the dotted line are accessible to the model.

Target Monitor

The target monitor was identical to the cursor monitor, except in that it lacked any motor output. Thus, the estimate for the current time step was based only on the previous time step's estimate and the current time step's observation.

Tracker

The role of the tracker was to bring the cursor in line with the target, in terms of both position and velocity. The tracker took as its input the position and velocity estimates from the cursor and target monitors. It calculated the position error (target position minus cursor position) and the velocity error (target velocity minus cursor velocity). It then calculated the minimum time in which it could bring the velocity of the cursor in line with that of the target (assuming the target velocity remained constant), given the maximum available acceleration. From this, it calculated the acceleration required to bring the position of the cursor in line with that of the target (again assuming constant target velocity), namely twice the position error, divided by the square of the minimum time to equalize velocity. This acceleration was output as the motor command.

Perceptual Adaptation Module

The role of the PAM was to monitor discrepancies between the expected sensory consequences of its motor actions, and the observed sensory consequences; and to compensate for those discrepancies appropriately. Thus, the PAM took as its input the last motor command sent by the tracker, and the correction made by the cursor monitor to its model of cursor velocity, based on the difference between its estimate and measurement. To obtain a point estimate of visuomotor misalignment, it took advantage of a rule of thumb. Assuming that acceleration is roughly constant over the timescale of the visuomotor misalignment, delayed consequences of motor actions would result in observed velocities falling short of expected velocities. For example, when accelerating rightwards with visuomotor delay, the observed visual feedback would reflect an earlier (less rightwards) velocity than the expected velocity. Again assuming that acceleration is roughly constant over the timescale of the delay, the size of the difference between observed and expected velocities should be equal to the acceleration multiplied by the delay. Thus, the ratio of the velocity correction (observed minus expected) divided by the last motor output would tend to be negative when sensory feedback was delayed. The negative of this ratio, then, was fed to a Kalman filter, which maintained an estimate of the misalignment on the basis of it.

This estimate of the misalignment was in turn used to alter the perception of any given sensory input. This was achieved by intervening in the measurement process of the cursor- and target- monitoring Kalman filters. The adjusted measurement sent to each monitor was extrapolated by taking the unadjusted measurement and adding to it the product of the misalignment estimate and the monitor's current estimate of the object's velocity. Thus, the model's perception was altered to compensate for any detected misalignment.

Parameters

Temporal and spatial resolution were chosen at levels appropriate for the human system that was being modelled. In the model, these are transparent and uniform, whereas in the human they cannot be fully characterized by single numbers. Nonetheless, approximate estimates of average spatial and temporal properties of the human visual and motor systems may be obtained.

Temporal Resolution

One measure of temporal resolution in vision is the critical fusion frequency (CFF). A CFF is a frequency below which motion would not be perceived as continuous, and - depending on various factors - has been reported in humans to be between 20 and 50 Hz (Landis, 1954). An alternative measure of temporal resolution is the double pulse resolution (DPR), which indicates how separated in time a pair visual stimuli must be to be discriminated from single visual stimuli. Thresholds of DPR, assessed using Treutwein's (1995) technique, were found by Poggel and Strasburger (2004) to be on average 50 ms (equivalent to a frequency of 20 Hz).

By measuring the lag between incorrect initial arm movements in a visuo-manual tracking task and subsequent online corrections, Cooke and Diggles (1984) obtained a measure that may indicate how soon motor behaviour can correct an action in response to a motor command error. Their results indicate that corrections may occur as soon as 30 ms after the error.

Thus, although one cannot assume that a single temporal resolution holds sway throughout the human visuomotor system, a temporal resolution of around 30 Hz would be of the same order of magnitude as typical estimates of the maximum frequency of both visual and motor response. This, then, was the value adopted in the model. Each time step would be equivalent to 1000/30 ms; twice the duration of each frame displayed on the computer screen in the experiments in Chapter 3.

Visuospatial Resolution

In visual perception, various measures of acuity are available. Wilcox's (1932) assessment of the range of resolution thresholds under different object illuminations found values ranging from around 30 seconds of visual angle to around 100 seconds with dimmer objects. The less acute end of this range would be equivalent to a distance of less than one pixel on a computer screen 30 cm distant from an observer's eyes, and thus no adjustment to the input stream of target locations was needed, relative to that which was used in Chapter 3's experiments.

Constraints

Maximum displacement from the origin was set as equivalent to the maximum displacement of the trajectory on the computer screen in Chapter 3's experiments. Maximum velocity was set at the mean maximum velocity observed for participants in Experiment 3.1 (84 pixels/frame, *SE* = 3; ranging from 31 to 194), and the maximum acceleration was set at the mean maximum acceleration observed (17 pixels/frame^2, *SE* = 9; ranging from 4 to 388).

Procedure

The procedure was identical to the exposure phase of a subset of Experiment 3.2. The semi-predictable target trajectory was used, and the only delay conditions were 0 ms and immediate exposure to 100 ms. Thus, there was a 2x2 design: exposed delay was either 0 ms or 100 ms, and the perceptual adaptation was either switched off or on. The model was run 10 times in each of the four conditions. The output of the perceptual adaptation module served in lieu of the perceptual aftereffects measure from Experiment 3.2. Behavioural measures were taken in the same manner as in Experiment 3.2.

Measures

The aim of the present study was to indicate whether the model could more effectively counter the direct effects of delayed sensorimotor feedback with a perceptual adaptation module than without. Thus, from the output of the model were derived measures of temporal inaccuracy and spatial imprecision for each trial, indicating how far the cursor lagged behind the target, and how variable its trajectory was after correcting for that lag, respectively. As in Experiment 3.2, for each of the two error measures, direct effects (first trial), error reduction (slope of trial in regression of the error measure) and incompleteness of adaptation (final trial) were calculated. Analysis of the error reduction measures indicated no impact of perceptual adaptation on error reduction (all *ps* > .1). This indicated that any effect of perceptual adaptation was present from the first trial onwards, if at all, and did not develop further; and so all further analysis was conducted on the mean values of the error measures, averaged across all 96 trials.

Results

First, the effectiveness of the perceptual adaptation module (PAM) was tested to confirm whether it was capable of detecting the misalignment, by comparing the average value of the model's representation of the misalignment between the 0 ms and the 100 ms condition. The model's mean estimate of misalignment in the 0 ms condition was 3 ms (*SE* = 1 ms), and in the 100 ms condition was 18 ms (*SE* = 1 ms). Thus, it successfully modelled 15% of the misalignment, compared with control, $t(18) = 11.7$, $p < .001$, $\eta_p^2 = .88$.

Further analyses were concerned only with the impact of the PAM on the two measures of error, in each of the delay conditions. As regards temporal inaccuracy, in the 0 ms condition, the PAM group (42 ms, *SE* = 4 ms) lagged non-significantly behind the no- PAM group (32 ms, *SE* = 5 ms), $t(18) = 1.7$, $p = .11$, $\eta_p^2 = .14$ (see Figure 4.1). In the 100 ms condition, the no- PAM group (188 ms, *SE* = 5 ms) lagged non-significantly behind the PAM group (PAM ms, *SE* = 5 ms), $t(18) = 0.7$, $p = .74$, $\eta_p^2 = .03$ (see Figure 4.2).

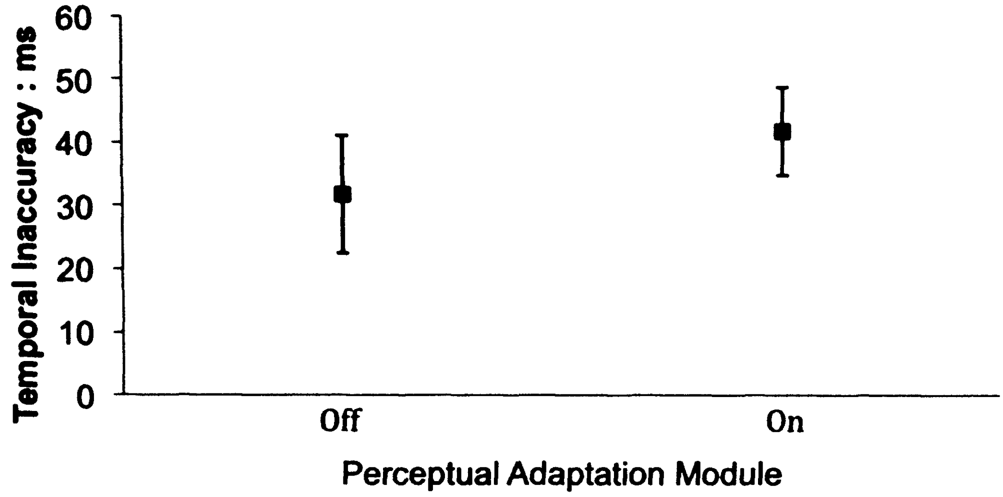

Figure 4.1 Mean (with 95% confidence interval) temporal lag of cursor behind target in the simulation model, in the 0 ms condition, with and without the PAM switched on.

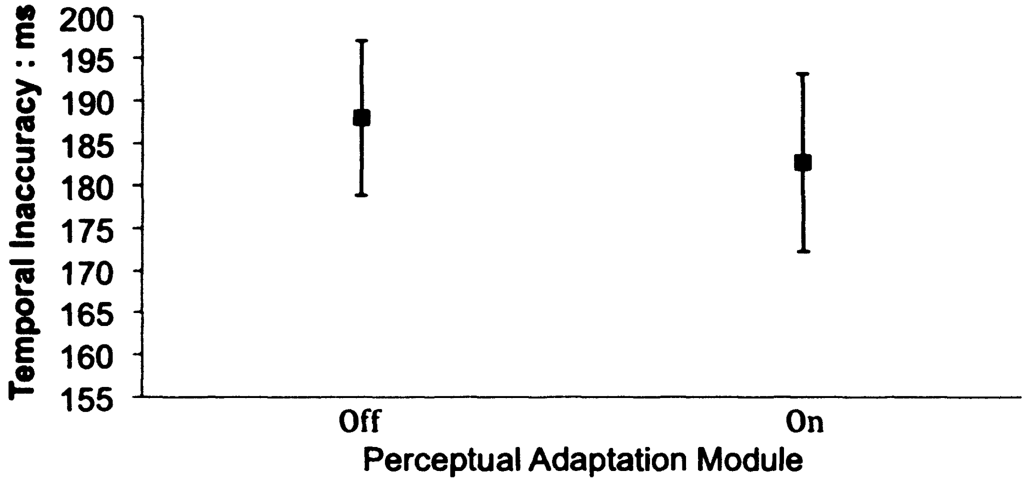

Figure 4.2 Mean (with 95% confidence interval) temporal lag of cursor behind target in the simulation model, in the 100 ms condition, with and without the PAM switched on.

As regards spatial imprecision, in the 0 ms condition, the PAM group (83 pixel, *SE* = 4 pixel) were significantly more imprecise than the no- PAM group (70 pixel, *SE* = 1 pixel) (see Figure 4.3); Levene's test indicated unequal variances, *F*(1,18) = 7.5, *p* = .01, so degrees of freedom for *t* were adjusted accordingly: *t*(9.6) = 3.2, *p* = .01, $\eta_p^2 = .37$.

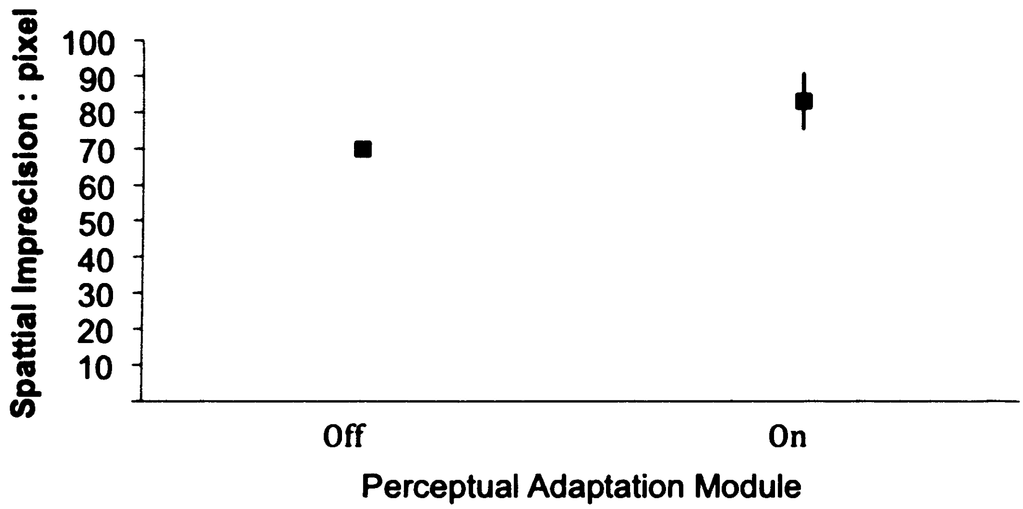

Figure 4.3 Mean (with 95% confidence interval) of spatial imprecision after correction for temporal lag of cursor behind target in the simulation model, in the 0 ms condition, with and without the PAM switched on.

In the 100 ms condition, the PAM group (144 pixel, *SE* = 5 pixel) were significantly less imprecise than the no- PAM group (236 pixel, *SE* = 0.3 pixel) (see Figure 4.4); Levene's test indicated unequal variances, *F*(1,18) = 41.0, *p* < .001, so degrees of freedom for *t* were adjusted accordingly: *t*(9.1) = 17.0, *p* < .001, $\eta_p^2 = .94$.

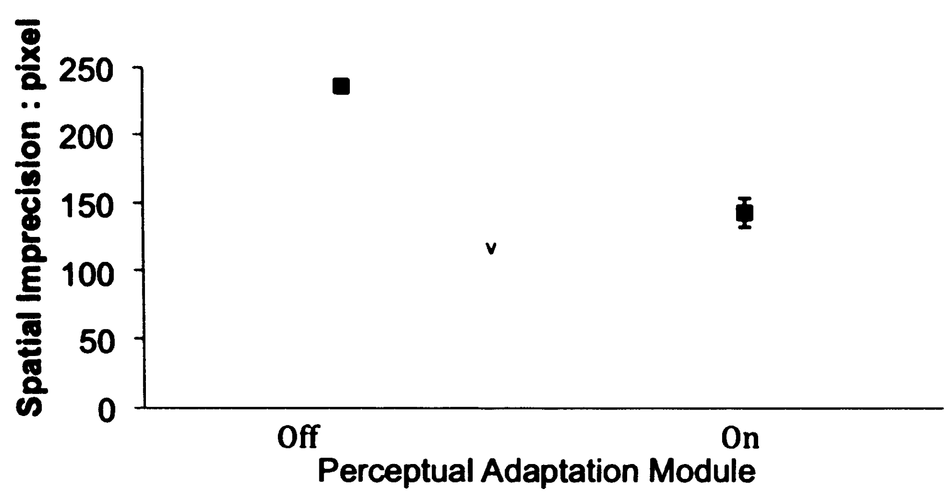

Figure 4.4 Mean (with 95% confidence interval) of spatial imprecision after correction for temporal lag of cursor behind target in the simulation model, in the 100 ms condition, with and without the PAM switched on.

Discussion

The perceptual adaptation module correctly detected the presence and direction of sensorimotor temporal misalignment in the 100 ms condition, and its response to it had the effect of reducing the spatial imprecision of its tracking. No such improvement was found in the temporal inaccuracy of its tracking. As argued in Chapter 3, perceptual adaptation may – in the face of relatively unpredictable targets – improve performance by reducing variable error despite being unable to anticipate the target sufficiently to remove the constant temporal error.

The model presented in this chapter provides a proof of concept that a simple, iterative rule of thumb can detect a sensorimotor misalignment, requiring only the most recent difference between its expected and observed velocity and the most recent efference copy of its motor action. Furthermore, by using this estimate to modify its perceptions (its observations of itself and the target), the model was able to reduce the imprecision of its tracking. Thus, it seems plausible that visuomotor temporal perceptual adaptation could be both possible and advantageous. It is interesting, therefore, that this result is at such odds with the human results from Chapter 3. With the same task, humans adapted their temporal lag behind the target, but not their imprecision; whereas the model did the reverse. A tentative implication of this is that participants did not adapt perceptually in Chapter 3, regardless of the ability of the criterion tasks to pick up on such adaptation.

However, any implication of the model's results at this stage must indeed be very tentative. It is, as yet, quite limited. The main limitations of the model are twofold. First, it has only a control module serving motor output and a perceptual adaptation module serving perception. To draw clearer conclusions about the usefulness of perceptual adaptation in visuomotor coordination tasks with temporal misalignment, one would need to incorporate and test a range of behavioural modules, grounded in empirical work on human tracking performance.

A second major limitation concerns the parameters of the model. The parameters governing spatial and temporal resolution were drawn from literature not directly relevant to the visuomotor task being modelled here. Empirical work to determine these parameters in the context of the task could provide a more accurate simulation of human performance. The parameters governing the covariance matrices of the Kalman filters, and the noise inputs to the model (see Appendix) were set offline, by trial and error, to ensure that the filters were neither inflexible nor liable to diverge or vary wildly over short periods of time. This particular limitation (the relatively arbitrary choice of covariance matrices) would prevent the model from speaking to any question of the time-course of adaptation, because that time-course would be governed by the exact values of those parameters. Again, more empirically grounded choices could improve the model's value as a simulation.

Nonetheless, this model has the capacity to provide qualitative predictions about the behavioural responses to a range of tracking stimuli with or without a simple perceptual adaptation module. It provides evidence that a simple recursive estimator may detect the direction, at least, of a visuomotor misalignment, and that using that estimator's output to modify the model's observations can reduce imprecision in tracking with delayed feedback. Moreover, it is a framework within which a variety of control strategies may be tested against a variety of possible mechanisms for perceptual adaptation.

Chapter 5: General Discussion

> "[...] and if you knew enough and could move faster than light you could travel backward in time and exist in two places at once."
>
> Margaret Atwood - *Cat's Eye*

I have presented a series of experiments to investigate the nature of the adaptive response to visuomotor temporal misalignment in time-critical visuomotor coordination tasks. As with visuomotor spatial misalignment (see Redding et al., 2005, for a review), direct effects and performance improvement were noted, except when the size of the misalignment was too great, or the stimulus trajectory was too unpredictable. However, perceptual criterion tasks to assess the perceived temporal alignment of visual and motor time revealed no temporal adaptation effects. Thus, the analogy with adaptation to visuomotor spatial misalignment appears not to hold. There are, broadly, two possible reasons for the analogy breaking down, which will be further subdivided: either perceptual adaptation is not evoked by the range of exposure tasks used, or perceptual adaptation is not detected by the criterion tasks used. I shall consider each possibility in turn.

Why No Perceptual Adaptation?

Perceptual Adaptation is not Evoked by the Exposure Tasks

The first possibility may be subdivided. It could be a feature of any task in which motor actions are timed relative to delayed visual information (or, equivalently, in which delayed motor actions are timed relative to non-delayed visual information), that perceptual adaptation is not evoked. Alternatively, there may exist other visuomotor coordination tasks, outwith the range explored in this thesis, that would evoke perceptual adaptation. Furthermore, for either of these alternatives, the failure to realign may be because it would not be advantageous to do so, or because, although it would be advantageous, the brain is incapable of doing so.

Whether perceptual adaptation would be advantageous in a visuomotor coordination task may be investigated by testing computational models of behavioural and perceptual adaptation to assess whether perceptual adaptation could produce advantageous performance improvement. If such a model predicted that perceptual adaptation would be more beneficial than the best plausible behavioural solutions, that would provide a proof of concept that would undermine the suggestion that behavioural adaptation is preferred in visuomotor coordination because it is more effective at reducing error.

To distinguish whether the lack of perceptual adaptation found in visuomotor coordination tasks reflects a general feature of visuomotor coordination tasks, one must consider whether the range of exposure tasks used thus far sufficiently reflects the range of normal visuomotor experience as to be a fair test of adaptation to visuomotor misalignment. If theoretical considerations or the results of modeling suggest that different tasks may either be more likely to promote perceptual adaptation or more likely to be benefit from it, further empirical work will be needed to disambiguate these possibilities. However, I believe that a reasonable range of tasks has been used in this thesis.

Tasks were used varying from Experiment 3.1's 'predictable trajectory' condition, in which the 100 ms delay could be compensated for so quickly as to prevent direct effects from being detected in the first trial, to Experiment 3.0's 'unpredictable trajectory' with 300 ms delay, in which no compensation was demonstrated at all. Thus, whether excessive unpredictability (over the timescale of the exposed delay) or excessive predictability (allowing easy behavioural compensation) would undermine perceptual adaptation, I have assessed behaviour and perception along a range of tasks between the two extremes.

Exposure tasks involving rich, complex two-dimensional trajectories (Experiments 3.0, 3.1 and 3.2) have been used, as well as tasks involving simple one-dimensional trajectories (Experiments 2.2, 3.1, and 3.2) that coincide fully with the spatial range of the criterion task stimuli. Visual feedback in the exposure tasks has been in the same aeroplane as the motor action (Experiments 2.0, 2.1, and 2.2), or rotated 90 degrees on to a computer screen (Experiments 1.0, 3.0, 3.1 and 3.2). Therefore, in these matters at least, it is likely that a sufficient range of exposure tasks was used. However, it might be that insufficiently long exposure tasks were used (the longest being Experiment 3.0's, at around 30 minutes). This is indeed possible, but the literature on spatial and temporal adaptation would suggest otherwise. Exposure phases of around three minutes have produced perceptual aftereffects in intersensory temporal adaptation (e.g. Fujisaki et al., 2004) and in visuomotor spatial adaptation (e.g. Redding & Wallace, 1994).

Perceptual Adaptation is not Detected by the Criterion Tasks

The alternative class of explanations is based on the idea that perceptual adaptation may have taken place in at least one of the experiments reported, but that the criterion tasks used for assessing that adaptation were unable to detect it. One possible reason why a criterion task might not pick up on adaptation is if the muscles or range of visual stimulation involved in the criterion task were not identical to some of those that adapted in the exposure task.

In all the studies reported in Chapters 1,2, and 3, the criterion task involved making quasi-sinusoidal movements from a centred position sideways, and back to centred[1]. All of the exposure tasks involved such left-right quasi-sinusoidal movement too, although the two-dimensional tracking trajectory used in Experiment 3.0 and in some conditions of Experiments 3.1 and 3.2 additionally involved an equivalent quantity of exposure to back-forth movement. Thus, the muscles used in the pre-test and post-test were always a subset of those exposed to delayed visual feedback in the exposure phase. Furthermore, the visual stimulation in the criterion task was the same as the visual feedback of motor activity used in the exposure tasks: in Experiment 2.2's task, a red laser spot; and in Experiment 3.0, 3.1 and 3.2's tasks, a white square. In all cases, the visual stimulation in the criterion task was placed within the range of locations exposed during the exposure phase. Therefore, it seems implausible to suggest that a difference in the involved muscles or range of stimuli can explain the lack of visuomotor perceptual adaptation.

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[1] Two other criterion tasks were explored, to investigate whether different combinations of motor actions would be more effective at detecting perceptual aftereffects. One involved initiating a movement away from centre, and judging the relative timing of the start of the movement and the start of an equivalent visual movement on the screen. The other involved intercepting (without visual feedback, as always) a moving target at the centre of the screen and then judging which arrived at the centre first. Neither of these criterion tasks produced notably different results to the one retained, except that the one I retained produced slightly less variable data.

Separate visual pathways for judgment and action? Even though the same muscles and visual areas were involved in the criterion tasks as were exposed to the visuomotor misalignment, it remains possible that the criterion tasks were tapping something other than the representations that would have been affected by perceptual adaptation during exposure. During exposure, visual information was being used to govern motor actions; whereas, during the criterion tasks, visual and motor information were being used to arrive at judgments about their perceived order. Differences in how visual information is used for action and for judgment have been reported. For example, Aglioti, de Souza, and Goodale (1995) used the Ebbinghaus size-contrast illusion (in which a circle's size is misperceived as smaller when surrounded by larger circles, and *vice versa*), and found that participants made grip apertures with their hands closer to the right size for the veridical (not the perceived) size of the circle. This result was used to support the claim that distinct neural pathways may subserve vision for action and judgment (e.g., Aglioti et al., 1995; Króliczak, Heard, Goodale, & Gregory, 2006). Aglioti et al. (1995) identified the suggested action and judgment (or 'prehension and apprehension', Goodale & Milner, 1992) pathways with the dorsal (originally proposed to code location by Schneider, 1969) and ventral (originally proposed to identify objects by Schneider, 1969) visual streams, respectively.

If visual information, when used to inform judgments, follows a different neural pathway (ventral) from that used for visuomotor coordination (dorsal), it is possible that any perceptual adaptation during exposure impacted only on the dorsal stream and would not be detected by any judgment task, tapping the ventral stream. Perception for action would have been altered, leaving perception for judgment unchanged. This would account for the dissociation between the lack of perceptual aftereffects of misalignment in the visuomotor coordination tasks used in the present work, and the perceptual aftereffects found in the visuomotor non-coordination task used by Stetson et al. (2006). In Stetson et al.'s (2006) study, motor actions had visual consequences, but they were not governed by visual stimuli. Participants simply made button presses, and flashes occurred at various times in relation to the button presses; visual information was only ever used for judgment, or not at all. Thus, Stetson et al.'s (2006) exposure trials may have tapped the same, ventral stream as the criterion trials.

However, if this explanation could account for the lack of measured perceptual adaptation in the present work, it could not account for the commonplace detection of perceptual adaptation in the response to spatial visuomotor misalignment. Typical exposure tasks in the literature on adaptation to prisms involve visuomotor coordination: The motor action produced during exposure depends on the spatial features of the visual stimuli presented. Vision is thus used for action in prism exposure tasks, and for judgment in prism criterion tasks; and yet perceptual adaptation is detected. Furthermore, the interpretation of the evidence on which is based this explanation in terms of separate pathways for action and judgment (e.g. Aglioti et al., 1995), has been the subject of some disagreement. Franz, Gegenfurtner, Bülthoff and Fahle (2000) noted that Aglioti et al. (1995) had, in the visual judgment task, asked participants to compare two simultaneously presented (one large, one small) Ebbinghaus illusion stimuli; whereas, in the visual action tasks, participants had to grasp only one circle. Franz et al. (2000) found that perceptual judgments when comparing two stimuli simultaneously showed a larger illusory effect on perceived size than the sum of the effects on the perception of each stimulus measured separately. Thus, they argued, the smaller effect on grip apertures than on perception found by Aglioti et al. (1995) could actually be explained as a superadditive effect of combining two illusory stimuli.

Act now: There is no time for perception. An alternative explanation of Aglioti et al.'s (1995) results (and other findings of perception/judgment dissociations; see Carey, 2001, for a review) has been put forward by Smeets, Brenner, de Grave, and Cuijpers (2002). Smeets et al. (2002) proposed that, whereas the Ebbinghaus illusion affects the perceived size of a circle, the spatial information used to grip a circle could be the distance between two positions on the circle. Consistent with this, Jackson and Shaw (2000) found that the force applied to an object was affected by the Ponzo size perception illusion, in line with its effect on judged size, whereas the size of the grip aperture was not. The overall size of an object would be the information more relevant to the force required than any distance on it, and thus the illusion-affected information was used to determine the grip force. Visuomotor action is effected rapidly, Smeets et al. (2002) argued, as soon as the relevant perceptual information required for the action becomes available. When one asks for an explicit judgment to be made, more time has passed in which to process the information further, and combine it with other information as it becomes available to give a single, coherent report. Consistent with this, Yamagishi, Anderson, and Ashida (2001) found that the illusion of a window's displacement in the motion direction of an object within it is larger for visuomotor measures than for perceptual judgment measures. That perceptual judgment tasks sometimes detect larger illusory effects than visuomotor tasks, Smeets et al. (2002) attributed to illusions having a longer history of investigation as illusions of perceptual judgment than as illusions of visuomotor response. Thus, the illusions that are known about and used to study judgment/action dissociations tend to be the ones that show a strong effect on judged perception; hence judgments sometimes showing larger illusory effects than actions.

Thus, under this account, judgment and action depend on the same information, but action is based in a timely fashion on a more limited subset of it, whereas judgment can at a more leisurely pace resolve and combine multiple inconsistent data (Smeets & Brenner, 2008). Can this dissociation between judgment and timely action explain the difference between, on one hand, sensorimotor temporal adaptation in a time-critical coordination task and, on the other hand, all other forms of sensorimotor (and intersensory) adaptation? I believe it can, but it may do so in one of two ways. I introduced this idea in a subsection within the discussion of the explanation that – whatever perceptual adaptation took place during exposure – the criterion tasks were unable to detect it. I introduced it because it could provide a reason for the criterion tasks failing to detect a perceptual aftereffect in temporal visuomotor coordination only. But it could also provide a reason for the exposure task failing to produce perceptual adaptation. Thus, I discuss both possibilities in the next section, before considering whether one can choose between the two of them.

Does the Dissociation Between Judgment and Time-Critical Action Explain the Results?

The judgment/action dissocation suggested by Aglioti et al. (1995) can explain the dissociation between the present work on temporal adaptation in visuomotor coordination and the literature on temporal intersensory (and visuomotor non-coordinative) adaptation. However, it cannot explain the dissociation between the present work and the literature on spatial visuomotor coordination. But the dissociation between judgment and specifically time-critical action can. Consider three types of task: time-critical visuomotor coordination tasks (tasks in which temporal features of a stimulus govern the motor actions selected, and in which the execution of the actions cannot be slowed down; such as any of the exposure tasks used in this thesis); time-uncritical visuomotor coordination tasks (tasks in which non-temporal features of a stimulus govern the motor actions selection, and in which there is sufficient time to consciously perceive the stimulus before initiating an action, and consciously perceive one's own action before completing it; such as any spatial adaptation exposure task); and finally, non-coordination tasks (tasks in which motor actions – if any – are not guided by temporal or spatial features of stimuli, let alone in a time-critical way ; such as any intersensory exposure task or a visuomotor non-coordination task such as that used by Stetson et al., 2006). In the last of these three, the non-coordination tasks, there are no for-action percepts involved in the task. In the first of them, the time-critical coordination tasks, there is little or no opportunity for the involvement of resolved for-judgment percepts in the exposure task. In the second of the three, the time-uncritical coordination tasks, there may be an intermediate amount of involvement of for-judgment percepts involved. For example, in a reaching to target task, such as is commonly used in spatial adaptation, there may be opportunity to form a resolved conscious percept of a visual stimulus prior to selecting an action, and may even be opportunities for monitoring and correcting the action before it has any effect on performance. In contrast, in a time-critical coordination task, such as was used in the present work, motor actions must be selected rapidly in the face of constantly (and in many conditions, relatively unpredictably) changing visual stimulation.

One possible application of the judgment/time-critical action distinction to the results of this work is to argue that perceptual adaptation is evoked by the exposure tasks, and is applied to those representations accessible to rapid online motor control. In the criterion tasks, participants access various sources of information about the timing of visual events and of their motor actions, perhaps including those for-action representations, but also including representations that have been processed further, for judgment. Thus, the resolved percept accessed in the criterion task would show a weakened or non-existent effect of any perceptual learning adaptation of for-action representations.

An alternative possibility is that perceptual adaptation is the business only of resolved, consistent perceptions for judgment, not of rapid, fleeting perceptions for action. Perhaps it is not meaningful, even, to speak of the perceptual adaptation of for-action representations. Certainly, if one uses 'perceptual learning' to include only those experiences that are impact on judgment or conscious report, then perceptual adaptation of representations not accessible to judgment would be a contradiction in terms. How can the converse of perception be adapted perceptually? However, if one uses 'perceptual learning' as I, after Bedford (1993a), have, to refer to any learning that improves the accuracy or precision of sensory systems, whether or not the results of such learning are accessible to conscious judgment, such a claim becomes logically allowable. Percepts for action may be modified (perceptual learning), rather than the selection rules for actions for a given percept being modified (behavioural learning); and in each case the unrevised percepts may be inaccessible to conscious judgment.

How Can One Decide Whether Temporal Perceptual Adaptation Occurs in Visuomotor Coordination Tasks?

Thus, although the dissociation between time-critical action and judgments can provide a framework for considering the dissociation between the present results and those in the spatial and intersensory temporal adaptation literature, it cannot help to determine whether perceptual adaptation was involved but undetectable, or wholly absent. How then can one access the representations of motor and visual timing relevant to visuomotor co-ordination? If retrospective judgment is not necessarily a reliable source of information, perhaps only behavioural measures will be of use, equivalent to those used in exposure not only in terms of muscles involved and range of the stimuli, but also in the time-critical, visuomotor coordination nature of the task. But here is a double bind. Perceptual visuomotor adaptation may be inaccessible through visuomotor judgment tasks, but would be confounded with behavioural adaptation in a visuomotor coordination criterion task. Perhaps, then, one must return to more indirect methods of assessing perceptual visuomotor adaptation.

As I discussed in Chapter 0, persistence in time is a feature of perceptual adaptation noted in the literature on spatial visuomotor adaptation, when it is properly separated from behavioural adaptation. Thus, the results of Experiment 2.1 seemed to give indirect support for the presence of perceptual adaptation. However, as I acknowledged in Chapter 2, it is possible that behavioural aftereffects of temporal perceptual adaptation are less stable over time than is the case with spatial perceptual adaptation. Perhaps, then, our attention should turn to exposure performance. With such a rich and relatively unpredictable visuomotor coordination task as the one used in Chapter 3, one would not expect identical performance whether adaptation was effected behaviourally or perceptually, or by a combination of the two. Indeed, as I argued in Chapter 0, one might expect a reduction in variable error more than a reduction in the temporal lag itself, if perception were adapted. Consistent with this hypothesis was the performance of the model in Chapter 4, which – when a perceptual adaptation module was available – showed reduction in variable error but not temporal lag. That this did not occur in any condition of any of the experiments reported elsewhere in the thesis undermines the interpretation that perceptual adaptation occurred in exposure but was not detected in the post-test, being more consistent with the interpretation that perceptual adaptation was not evoked during exposure.

The tentative conclusion of the present work is, therefore, that no perceptual adaptation occurred during the exposure tasks used in this thesis; and that that explains the lack of perceptual aftereffects in the criterion tasks of Experiments 2.2, 3.0, 3.1, and 3.2. This conclusion is tentative not least because it is based to a great extent on the performance of a very limited simulation model.

A key avenue for further investigation is to develop this model to include, in addition to the perceptual adaptation module, a range of behavioural modules grounded in the literature on visuomotor tracking performance. This may lead to predictions of stimuli that would be more likely to elicit perceptual adaptation (or more likely to benefit from it). Additionally, it may be used to generate hypotheses about indirect indicators of perceptual adaptation in exposure (and post-exposure) behavioural performance.

Summary

In sum, a range of approaches to studying temporal visuomotor adaptation, grounded in the literature on spatial misalignment, has been examined. Where the visuomotor misalignment was sufficiently small, and the stimulus sufficiently predictable, this has resulted in behavioural, but not perceptual adaptation to temporal misalignment in visuomotor coordination tasks. This is in contrast to findings in the spatial literature, and in the temporal literature for intersensory and visuomotor non-coordination tasks. A possible reason for this discrepancy is that time-critical visuomotor coordination behaviour may rely on representations dissociable from those more processed representations available for retrospective judgments.

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Appendix: Kalman Filter Parameters

The parameters of the Kalman filters and the noise covariance matrices used in the model described in Chapter 4 were selected by trial and error, and were chosen to ensure that the filters were neither inflexible nor liable to diverge or vary wildly over short periods of time. Their values were as follows:

Target/Cursor monitor observation noise: [0.0001]

Target/Cursor monitor process noise: [0.0001 0

0 0.00001]

Perceptual Adaptation Module observation noise: [1]

Perceptual Adaptation Module process noise: [0.001 0

0 0]

Target/Cursor/PAM initial error covariance matrix: [0.2 0

0 0.2]