Synchronization with audio and visual stimuli: Exploring multisensory integration and the role of spatio-temporal information

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Authors Declaration

I hereby certify that this material, which I now submit for assessment on the programme of study leading to the award of Doctor of Philosophy is entirely my own work, and that I have exercised reasonable care to ensure that the work is original, and does not to the best of my knowledge breach any law of copyright, and has not been taken from the work of others save and to the extent that such work has been cited and acknowledged within the text of my work.

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Alan Armstrong (Candidate)

Acknowledgments

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Abstract

Information lies at the very heart of the interaction between an individual and their environment, which has led many researchers to argue that the coupling constraining rhythmic coordination is informational. In an attempt to address this informational basis for perception-action this thesis explored the specific information from a given environmental stimulus that is used to control our actions. Namely, participants in the three studies synchronized wrist-pendulum movements with auditory and visual stimuli with different spatio-temporal structures. The aim of this thesis was to establish the role of spatial and temporal information in the control of rhythmic actions.

Study 1 revealed that the presence of spatial information significantly improved synchronization with a continuous visual stimulus. Interestingly, the absence of spatial information still produced good levels of coordination indicating a resilience of motor coordination to adapt to changes in the environment. Study 2 expanded on these findings using an auditory stimulus, revealing that the supplementation of spatial information did not have a significant impact on synchronization with this modality. When these auditory and visual stimuli were combined in bimodal conditions there appeared to be no benefit over the unimodal conditions and instead there was a strong bias towards the visual stimuli in these multisensory conditions. The first experiment from Study 3 specifically addressed the role of perceiving relative direction for visual and auditory stimuli by partially occluding these stimuli. While perceiving relative direction at the endpoints of a stimulus' trajectory was important for both modalities, the auditory modality relied more heavily on this information. The second experiment revealed that when information is occluded in one modality another modality can effectively "fill-in" for the missing information and help to stabilise coordination.

The results from the three studies in this thesis clearly indicate that spatial information plays a different role in synchronizing with visual compared to auditory stimuli. These differences are more than likely related to the fact that spatial

information is more easily perceived with visual compared to auditory stimuli. Additionally, comparing the bimodal results from study 2 and 3 appears to indicate that the integration of sensory information for improving motor coordination may be mediated by task difficulty. Future research may look to address the specific role that task difficulty plays in multisensory integration.

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Chapter 1: Introduction to the Thesis

1.1 Publications and conference proceedings

Journal Articles:

Armstrong A, Issartel J, Varlet M, Marin L (2013) The supplementation of spatial information improves coordination. Neurosci Lett 548:212–6. doi: 10.1016/j.neulet.2013.05.013

Sullivan T, Zhang D, O'Connor E, et al. (2013) Improving data driven decision making through integration of environmental sensing technologies. Ocean. '13 MTS/IEE. pp 1–7

Armstrong A, Issartel J (2014) Sensorimotor Synchronization with Audio-Visual Stimuli: Limited Multisensory Integration. Exp. Brain Res.

In Preparation:

Armstrong A, Issartel J (in preparation) The Effect of Occlusion on Synchronizing with Auditory and Visual Stimuli. J Exp Psychol Hum Percept Perform.

Poster Presentations

Armstrong A, Issartel J (2013) Understanding Motor Coordination with Unimodal and Bimodal Stimuli: Vision and/or Audition? ACM Symp. Appl. Percept.

Oral Presentations

Armstrong A, Issartel J, Varlet M, Marin L (2011) Effect of Frequency and Visual Stimuli on Rhythmic Coordination. 16th Int. Conf. Percept. Action

1.2 Introduction

1.2.1 General Introduction

This thesis explores how humans interact with their environment. At a fundamental level this interaction takes place using both our perception of a given environment and our actions within the environment. These two central features of our interaction with our environment, perception and action, are inherently linked and directly influence each other. Their relationship is described as perception-action coupling, whereby a given perception of our environment can influence an action and this action in turn can influence the perception of the environment. For example, simply viewing a cup on a table that is within reach influences our actions since we know that we can pick up the cup. The action of picking up the cup in turn influences our perceptions, as we understand more about its weight, texture, temperature etc. This cyclical process of perception-action coupling relates to effectively all our interactions with our environment from simple to more complex tasks. Regardless of the complexity, perception-action coupling provides a fundamental basis for understanding how these tasks are performed, making this area of research extremely important in order to develop an understanding of how we interact with our environment.

Embedded in this cyclical relationship between perception and action is the information that is used to support the entire process. In order to set the context for this thesis it is important to explain what is meant by information and the role that it plays in perception-action coupling. Within the field of ecological psychology, Gibson (1986) helped to define what is meant by information from the environment and how it influences perception and action. Gibson viewed perception in terms of information pick-up, describing the process as the flow of energy from the environment that is “picked-up” by the various senses. For example, he defined visual information pick-up in terms of the optic flowfield, the continuous flow of light that is received by the eyes. From this perspective invariants and disturbances in the optic flowfield constitute the visual information that is perceived. While Gibson's work mainly focused on visual perception his concepts regarding information pick-up can also be used more generally with the other senses. Now that there is an established definition of information that is perceived from the environment, invariants and disturbances to the energy flow picked-up by our senses, it is important to explain how this information is used and the role that it plays in perception-action coupling. More specifically, what does this information specify in the environment that allows for humans to interact and move coherently.

Gibson (1986) linked information pick-up closely to both perception and action arguing that the information that we perceive through our various senses is what the environment offers or affords for action. The information picked-up by our senses essentially specifies opportunities for actions that we can complete. Gibson, (1986) coined this idea as an "affordance". For example a chair affords sitting and a cup within reach affords being grasped. Thus, the information from the environment is both meaningful for and specifically related to action (Kelso 1995). It plays a central role in perception-action coupling by allowing a person perceive the possibilities for action within their given environment. Importantly, the various characteristics of the information can have a significant impact on our perceptions and subsequently on our actions. These characteristics relate to the temporal and spatial aspects of the information as well as the specific modality that is used to perceive the information, i.e. vision or audition.

Perceiving is the fundamental basis for interacting with our environment and relies on information from multiple senses. The perception of this information allows for individuals to make sense of our environment (Rookes and Willson 2000). Depending on the individual context as well as the environment, the role of each of our senses varies. This reflects the idea that while each sensory modality is able to perform a variety of functions in relation to perception, they each possess particular strengths and weaknesses (Welch and Warren 1980). For visual and auditory perception these particular strengths relate to the spatial and temporal characteristics of the information that is being perceived. For example, we can perceive the movement of an animal through both visual and auditory information but as research has shown the perception of spatial information is superior for the former (Welch and Warren 1980). In contrast, audition is superior compared to vision in terms of perceiving time. Inherent in these strengths is the fact that no one modality provides a reliable perception of our environment all the time. Since the environment is constantly changing, different senses may be required depending on the circumstances. For example, while vision is quite important for navigating within our environment, at night when the saliency of this visual information is reduced, we are inclined to rely more on haptic or auditory information to move in our environment.

In our daily life, we perceive and integrate information from different modalities providing complementary information about a given event (Ernst and Bülthoff 2004). When this information is integrated, perceptual phenomena can often occur where one modality effectively alters the perception of another modality. Interestingly, these phenomena have been extensively used by the entertainment industry in order to provide the spectator with a more realistic experience. Take for example the well-known ventriloquist act where the performer appears to make a dummy talk on stage. Anecdotally, this is often explained as an ability of the performer to “throw” their voice towards the dummy but in actual fact it relates to a perceptual phenomenon. Due to the lack of movement in the performer’s mouth and the poor localisation of spatial information with audition, the movements of the dummy’s mouth “capture” the sound and it is perceived as coming from this location. Thus, the auditory information is coupled with the most likely visual event, i.e. the dummy moving its mouth. In a similar way, this phenomenon is constantly exploited in cinemas to compensate for the spatial disparity between the auditory and visual information where the continuous visual space (i.e. the large screen) is often coupled with only a small number of speakers dispersed near the screen (Väljamäe and Tajadura-Jiménez 2007). Despite the differences in the locations of the visual and auditory information the audience perceive the audio-visual information to be emanating from the same location.

This phenomenon can also occur in the reverse direction where the strength of the auditory modality is exploited in order to modify the perception of a visual event. During the making of *Star Wars: The Empire Strikes Back,* the director exploited the temporal strengths of audition in order to make a door appear to open (Chion 1994). In this case the director took two still shots: a closed door and an opened door. In the movie these two images are played in sequence along with a continuous "psssht" sound. The audience perceive the door as sliding open while, there is in fact only two discrete images being presented. In this case, the temporal aspects of the continuous sound are tightly coupled with the discrete still images of the door opened and closed, ultimately altering the perception of the doors continuity.

More importantly, these audio-visual interactions have also been used to enhance the overall experience of a given event. The tight coupling of auditory information with a movement on screen can help to enrich the particular scene. For example, fight scenes in movies often contain a series of rapid movements. In order to direct the attention of the audience towards particular movements, auditory information can be employed. This is clearly seen in Kung Fu movies where the rapid movement of punches are tightly coupled with rapid auditory punctuation. The idea is to emphasise and enrich these visual events by creating a strong audio-visual experience (Chion 1994). Similar effects are employed by Disney to enhance the movements of their animated characters. In this case, they use a method know as *mickeymousing*, which involves the pairing of visual actions with music in order to enrich these movements (Thomas and Johnston 1981). For example, ascending music often accompanies an animated character climbing up a hill in order to emphasise the spatial trajectory (Chion 1994). In this example, the congruency between the ascension in the sound and in the visual scene allows for this information to be integrated producing an enhanced experience for the audience.

In recent years, entertainment has begun to move towards a more immersive and interactive environment. This constitutes the use of virtual reality equipment where a person becomes part of a virtual environment. Virtual reality has been used in a variety of contexts and has important implications for rehabilitation (Cuthbert et al. 2014), creating indoor training environments for athletes (Filippeschi et al. 2009) and analysing specific skills in sport (Watson et al. 2011). In all of these settings, understanding how sensory information is integrated plays a key role in making these virtual realities perceivably realistic for the users. Researchers have begun to investigate how people perceive their environment so that the multisensory features of virtual reality can be optimally presented in order to create a temporally and spatially congruent perceptual world (Väljamäe and Tajadura-Jiménez 2007).

As previously shown, spatial and temporal information are perceived differently for audition and vision and the first aim of this thesis is to explore these differences. This thesis will look at how spatial and temporal information can impact actions in different ways depending on whether this information is picked up by vision or audition. While differences between these two modalities are know, as evidenced by the above text, within the field of perception-action this specific question has not been directly investigated. Thus, by focusing on this research aim this thesis will fill in the current gap in the literature relating to the perception of spatial and temporal information with vision and audition and the impact this may have on action. While all of the studies presented in this thesis relate to basic research, they may be of some relevance to other more applied or practical areas. Regarding the first aim of the thesis the main findings relating to this may be applicable to a number of specific areas. One of these areas relates to stimuli or signals that are used to warn a person of a specific imminent danger. For example, recent research has begun investigating an appropriate collision warning system for road users (e.g. Gray, Ho, & Spence, 2014). The main findings from this thesis could be a useful foundation in terms of both selecting the most effective modality for delivering the warning and in terms of how the signal is structured, i.e. its spatial and temporal characteristics. More importantly, this initial aim of the thesis provides an appropriate base for future research, which may aim to explore similar research questions with more “ecological” or realistic stimuli in order to establish if the underlying perception-action coupling remains the same for simple and more complex information or stimuli.

The findings relating to this initial aim directly feed in to the main aim of this thesis, which relates to multisensory integration. The main aim of this thesis is to explore how sensory information is integrated across two modalities, i.e. audition and vision, and how this integration may be effected by spatial and temporal information. By firstly establishing how spatial and temporal information influences the perception-action cycle with visual and auditory stimuli a comparison can then be made when the same modalities are presented concurrently. This comparison is important as it will be used to establish any changes in the perception-action cycle that may occur when information from multiple senses is integrated and importantly it will help establish if this integration has any benefits for action. Again, while this research is not directly aimed at having a practical or applied basis these findings may be of benefit to numerous areas. Firstly, the perception-action literature surrounding multisensory integration is limited, as will be highlighted in Chapter 2 Section 2.2.6, and the research questions focusing on this aspect of the thesis will serve to improve our understanding of how sensory information is integrated. Secondly, by expanding our knowledge of how we integrate information from different modalities it is possible that this could be used for enhancing different learning experiences. For example, during rehabilitation multisensory cues may be extremely useful for correcting or improving performance of a specific skill. The main findings from this thesis may be useful as a foundation for selecting the most appropriate multisensory stimulus in order to maximise the benefits of any number of learning experiences.

1.2.2 Aims and objectives of the thesis

This thesis aims to explore how different aspects of visual and auditory information can influence our actions by assessing a persons ability to synchronize movements with computer generated stimuli. Synchronization in this context refers to the ability of a person to adjust his or her own rhythm of movement to match that of a stimulus. A synchronization task was chosen as it represents an extremely effective way of assessing the perception-action cycle. We continuously synchronize our movements with different information or stimuli on a daily basis and this constitutes a main part of our interactions with the environment. By assessing the way in which we synchronize our movements with different types of stimuli it is possible to infer how this information affects the perception-action cycle (a more in-depth discussion surrounding synchronization can be found in Section 2.2.2).

The purpose of this thesis is to assess how temporal and spatio-temporal information influence the ability to synchronize with auditory and visual stimuli. Before addressing the integration of these stimuli with this information, it is important to examine these individual modalities separately. Study 1 (Chapter 3) focuses on the role of spatial information in a synchronization task with visual stimuli. While the perception literature points towards a dominance of vision with spatial information, this has not been specifically assessed in the field of perception-action. Thus, this first study aims to fill this gap in the literature by comparing synchronization of wrist-pendulum movements with temporal or spatio-temporal visual stimuli. Based on the evidence from the perception literature it is hypothesised that the synchronization task will be significantly better when spatio-temporal information is available compared to when only temporal information is available.

Study 2 (Chapter 4) focuses on similar questions but with both visual and auditory stimuli presented in unimodal and bimodal conditions. Currently, there is only a limited understanding of how spatial information is perceived and used in synchronization with auditory stimuli. Thus, the unimodal conditions serve to fill this gap in the literature and expand on the findings from Study 2 by addressing the specific role of spatial information in stabilising coordination with an auditory stimulus. It is firstly hypothesised that the results relating to the visual stimuli will confirm the findings from study 1. Secondly, it is hypothesised that the synchronization task will be significantly better with the visual compared to auditory conditions overall. Thirdly, it is hypothesised that for the auditory conditions the performance of the synchronisation task will be similar for the spatio-temporal and temporal stimuli. Research to date has not specifically focused on how temporal and spatio-temporal information can influence the integration of sensory information in synchronization. The auditory and visual stimuli were also presented simultaneously with different combinations of temporal or spatio-temporal information in order to assess how these specific characteristics would influence synchronization. It is hypothesised that the synchronization task will be significantly better with the multisensory conditions compared to the unisensory conditions, which would indicate a benefit of sensory integration. It is also hypothesised that within these multisensory conditions the synchronization task will be significantly better when spatio-temporal information is available in both modalities compared to when temporal information is available in one or both modalities.

Study 3 (Chapter 5) has two main objectives, the first of which was to assess the role of perceiving relative direction for auditory and visual stimuli. These two modalities were presented in unimodal conditions where the stimuli were occluded at different locations and by different amounts. While it is known that the perception of relative direction at the endpoints of a moving visual stimulus is essential for stabilising synchronization, little is known about how coordination is stabilised with a moving auditory stimulus. Thus, the purpose of the first experiment was to address this gap in the literature by comparing occlusion with auditory and visual stimuli. Firstly, it was hypothesised that the performance in the synchronization task will be better overall with the visual compared to the auditory stimuli. Secondly, it was hypothesised that occlusion at the endpoints of the auditory stimuli would result in a significant decrease in performance compared to the other occlusion locations. Thirdly, it was hypothesised that the results relating to the visual stimuli would corroborate previous work using a similar methodology (e.g. Hajnal, Richardson, Harrison, & Schmidt, 2009).

The second objective was to address the “filling-in” effect (see *Star Wars* example above) using auditory and visual information. The aim was to assess whether occlusion in one modality could be “filled-in” with information from another in order to help stabilise motor coordination. Similar occlusion amounts and locations were used with the three different multisensory stimuli; visual occluded with auditory non-occluded, visual non-occluded with auditory occluded, both visual and auditory stimuli occluded. It was firstly hypothesised that occlusion in both modalities would produce significantly worse performance compared to when only one modality was occluded. Secondly, it was hypothesised that performance in the synchronization task would be better when the visual stimulus was not occluded.

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Chapter 2: Review of Literature

2.1 The perception of auditory and visual stimuli

2.1.1 Introduction to perception

Within the field of ecological psychology, perception and action are tightly coupled together. The nature of this interconnectedness is cyclical since perception can inform action while actions can alter perception. For example, if we perceive a small object, say a stone, on a table this perception informs our action and the object can be picked up. While moving toward this object, additional perceptual information is gained, such as the size and shape, which highlights how action in turn informs perception completing the cyclical process. Notwithstanding the important connection between perception and action, which will be fully addressed in Section 2.2, research has also focused on understanding how we perceive our environment independently of performing actions. While Gibson's (1986) view towards perception implies that the information from the environment always relates to action, separating these two elements motivates some researchers to try to establish what and how we perceive our environment before trying to explain how it impacts on action. In this context, research within the field of perception aims to establish how perception is formed, namely the specific information from the environment or a stimulus that is used by the perceptual system, as well as the key perceptual differences between information from different sensory modalities.

Before delving into this research it is important to establish a definition of perception. According to Gibson’s perspective perception is essentially the act of picking up information continuously from the environment, more specifically perceiving is a registering of changes within the environment (Gibson 1986). However, it is important to note that according to this theory perception does not strictly occur in the nervous system rather it is a process in the animal-environment system (Kelso 1995). Essentially perception provides a necessary link between the animal and its surrounding environment. In other words, perception relates to how we make sense of our environment (Rookes and Willson 2000) allowing us to attach meaning to sensory stimuli (Haywood and Getchell 2005). The research discussed below will address the specific information that is used in the perception of auditory and visual stimuli as well as highlighting the different characteristics of each of these modalities.

2.1.1.1 The importance of spatio-temporal information

Changes occur in our environment constantly as events evolve over time and space. The ability to perceive these changes is a crucial aspect of survival for humans and constitutes the perception of spatio-temporal events (Nijhawan and Khurana 2010). These events occur at a specific time or have a specific duration, providing the *when*, and take place at a specific location or across various locations if motion is involved, providing the *where*. Our nervous system is even designed to detect these key properties of stimuli (Nijhawan and Khurana 2010), providing a unique grounding for our perceptual system. Information relating to both of these properties, namely space and time, is required for real-time sensorimotor control (Dominey et al. 1997), thus, space and time are naturally connected (Nijhawan and Khurana 2010), It is known that auditory information plays an essential role, for example, in alerting a person of potential dangers (Zanker 2010) and in this context both spatial and temporal information are utilised. For example, when we hear a loud bang, something that may signal danger, we assess temporal aspects of the sound that can help determine what created the sound, how heavy it was, as well as the spatial aspects, finding the location of the bang and how far away it occurred in order to assess the danger. The importance of spatial and temporal information is also highlighted by the extensive amount of perception research, which has focused on these properties, specifically with visual and auditory stimuli. The information for auditory and visual stimuli are fundamentally different, sound and light respectively, thus the way in which they are picked up by the perceptual system also differs. As a consequence of these differences the perception of visual and auditory information is not the same and each of these modalities possess particular strengths in terms of spatial and temporal information, respectively As previously mentioned perception is closely linked to action and the purpose of the following sections is to provide a basic understanding of the perception of visual and auditory stimuli which will help to inform the later discussion in Section 2.2 on perception-action coupling. Specifically, the following two sections will address the role of spatial and temporal information in modifying the perception of visual and auditory stimuli, highlighting their individual strengths and examine how these modalities are integrated to create a unified percept.

2.1.2 Visual and auditory perception

One of the most common paradigms in the perception literature involves cross-modal interactions, which are used to explore the particular strengths of a given modality within the temporal or spatial domain. In this paradigm often the objective for the participants is to pay attention to one specific modality while a distractor stimulus from another modality is also present. The level of influence that this distractor stimulus can have on the perception of the attended modality is used as a measure of both the integration of sensory information, which is addressed in Section 2.1.3, and the strength of this modality within a given domain. Stemming from this paradigm are several key perceptual phenomenon that help to develop an understanding of how these modalities are perceived as well as demonstrating the particular strengths that are inherent with auditory and visual stimuli. One of the most common forms of perceptual phenomenon is known as the *ventriloquism effect* (Howard and Templeton 1966) where by the presence of one modality effectively “captures” the other modality in terms of altering the perception of a given event or stimulus. Importantly, this effect has been shown to exist in favour of both visual and auditory information but in different domains.

2.1.2.1 Visual perception

Visual stimuli are known to have a significant impact on the perception of auditory stimuli specifically in terms of spatial perception. This research emphasises the superiority of the visual modality in the spatial domain. This dominance of visual stimuli within a spatial context is exemplified with the *spatial ventriloquism effect* a perceptual phenomenon first reported by Howard & Templeton in 1966. This phenomenon involves the presentation of a visual stimulus that can capture the location of an auditory stimulus. Essentially this effect pulls the perceptual system towards the location of a visual stimulus when both are presented at the same time. The implication here is that the perception of the event is more heavily weighted towards the visual modality, clearly displaying the dominance of visual information in the spatial domain. Alais & Burr (2004) investigated the effect of saliency of a visual stimulus on the ventriloquism effect. In their study participants observed brief simultaneous presentations of a visual blob and an auditory click and were asked to state which stimulus appeared more leftward. For their salient visual stimulus the results indicated the presence of the ventriloquism effect as participants were biased towards the visual stimulus when the locations of both stimuli were incongruent. These results are in support of the high spatial perception for vision and indeed the dominating effect that this visual stimulus can have on the perception of other stimuli. Other research using slightly different methodologies have also provided support for the spatial dominance of visual information.

For example, research by Kitajima & Yamashita (1999) investigated the influence of a moving visual stimulus on the perception of both a moving and stationary auditory stimulus. The key difference with this study and Alais & Burr (2004) is that the former used stationary as well as dynamic auditory and visual stimuli. In their study participants were required to judge the direction of movement of a sound with different orientations such as stationary (no movement), horizontal, vertical and in-depth movements. Visual moving stimuli were also presented with the same or different orientations. The overall results indicated that the perception of auditory motion was significantly influenced by the direction of the visual motion, even when the auditory stimulus was stationary. Additionally, it has also been shown that even when the two modalities are presented sequentially the spatial influence of the visual modality still affects audition. This was shown by Kitagawa & Ichihara (2002) who found an aftereffect in participants after viewing a visual stimulus that moved in depth. Following a period of viewing this visual stimulus, participants perceived a stationary auditory stimulus as changing in loudness showing a clear influence of the visual modality in terms of spatial perception. Both of these studies clearly support and extend the findings from Alais & Burr (2004) showing the dominance of visual stimuli in terms of spatial perception is not limited to localisation but also includes motion perception. Knowing the strength of the visual modality in terms of spatial information is important as it can help inform experimental designs in the area of perception-action. For example, despite the extensive research supporting the importance of spatial information for vision little or no research has directly addressed this within the context on perception-action. Study 1 (Chapter 3) of this thesis aims to investigate the importance of spatial information in a visual motor coordination task by comparing synchronization with a temporal and spatio-temporal visual stimulus effectively expanding on the perception research and bridging the gap with perception-action.

2.1.2.2 Auditory perception

In contrast with the high saliency of spatial information within the visual system, audition is more accurate with temporal rather than spatial properties (Spence and Squire 2003; Ernst and Bülthoff 2004). As a consequence of this strength much of the literature has focused on temporal properties with this modality. It has been well established that temporal acuity is better with audition than vision (Alais and Burr 2004) and the strength of temporal acuity with audition is evidenced by the *temporal ventriloquism* effect. This phenomenon is very similar to the *spatial ventriloquism* effect discussed above except in this case an auditory stimulus captures a visual stimulus (Burr and Alais 2006). Although similar effects of auditory stimuli on visual judgments have been reported previously this specific phenomenon was first reported over ten years ago by a group of researchers investigating whether irrelevant sounds could influence the perception of visual stimuli (Morein-Zamir et al. 2003). In the first experiment of their study participants were required to view two visual LEDs (top and bottom) and judge which of the two flashed first. These visual stimuli were accompanied by a sound that proceeded and followed the first and second visual stimulus, respectively. The results of this experiment indicated that the presence of the sounds enhanced visual judgement. The subsequent experiments in their study even ruled out any effect of alerting the visual system that may have been caused by the auditory stimulus. Ultimately their research provided the first reported evidence of this *temporal ventriloquism*, which supports the high temporal acuity of auditory stimuli. Other research has also found similar effects of temporal judgments with visual stimuli when auditory stimuli are also present.

For example, research by Burr, Banks, & Morrone (2009) assessed the temporal localisation of auditory and visual stimuli using a bisection task. In this experiment participants were presented with three stimuli in succession and were asked to judge if the middle stimulus was closer to the first or third stimulus. Their results indicated that when auditory and visual stimuli were presented together but with temporal conflict, the auditory stimulus dominated over the visual stimulus for the perception of timing. This temporal strength of auditory stimuli was also evidenced in a simple perception task where participants were required to judge the number of flashes from a visual stimulus (Shams et al. 2000). In this study the flashes were accompanied by an auditory stimulus that was to be ignored but beeped at the same or higher rates than the visual stimulus. Their results again supported the dominance of auditory information for temporal perception since when the flashes were accompanied by a greater number of beeps participants perceived a higher number of flashes in the direction of the auditory stimulus. As highlighted by the authors, this result is quite important since it represents a quantitative change in the visual perception by an auditory stimulus. This dominance of auditory stimuli in the temporal domain has as been shown to influence the perceived continuity of a visual stimulus. In their study, Väljamäe & Soto-Faraco (2008) assessed how an auditory stimulus could modify the perceived continuity of a visual stimulus. Participants viewed a series of visual flashes that increase in depth accompanied by a series of auditory beeps that increase in loudness. The individual modalities were presented at high or low rates, corresponding to shorter and longer intervals between discrete presentations respectively. Their results indicated that participants viewed the visual stimulus as continuous when the flash, presented at a low rate, was accompanied by a high rate auditory stimulus extending the support for auditory dominance in the temporal domain to include the perception of continuity.

2.1.2.3 Vision and Audition: Complementary sensory modalities

Overall these results provide strong support for the individual strengths of visual and auditory stimuli in the perception of spatial and temporal information, respectively. These studies not only provide an insight into the perceptual strengths of these modalities but also provide a deeper understanding of cross-modal integration of sensory information. This integration of information from different modalities is an effective way of finding the most reliable and robust interpretation of a percept (Alais et al. 2010) since information from different modalities can provide complementary information about a given event that is being perceived (Ernst and Bülthoff 2004). The combining of this information from multiple modalities helps to disambiguate a given percept when one modality does not provide enough information to create a robust percept (Ernst and Bülthoff 2004). For example this complementarity of different sensory information has been shown in object recognition tasks (Newell et al. 2001). In this study it was shown that the visual system tends to recognise a three-dimensional object from the front view while haptic information generally recognised the same type of objects from the back. When integrated together these two modalities clearly provide complementary information about a given object from different viewpoints improving the overall perception of this object. In a similar sense, combining the temporal acuity of audition and spatial acuity of vision may enhance the perception of a given event. This leads on to the concept of multisensory integration, which has already been indirectly touched on above. The next section will discuss the concept of multisensory integration in more depth and will highlight some of the key theories relating to how some researchers believe the perceptual system integrates information from different modalities.

2.1.3 Multisensory integration

In order to create a robust perception of our environment information from difference senses needs to be combined, creating a unified percept (Burr and Alais 2006). Often this information is complementary and can improve the overall perception of a given stimulus or event, as highlighted previously (See Newell et al., 2001). Indeed, it has been well established that for stimuli relevant to a given task multisensory integration serves a purpose of improving the perception of events (Rowland et al. 2007; Shi and Müller 2013). The relevance of the stimuli can relate to several factors with temporal coincidence being one of the most important. This temporal coincidence, specifically for auditory and visual stimuli, is key for multisensory integration, probably to accommodate the differences in how these modalities are picked up by the perceptual system (Alais et al. 2010). Thus, for audio-visual integration to occur it must be within a temporal window which is around 100 ms (Lewald et al. 2001; Shams et al. 2002). This was evidenced in the results from Shams et al. (2000) where the ability of multiple beeps to alter the perception of a lower number of visual flashes diminished once the two modalities were temporally incongruent by more than 70 ms. Therefore the perceptual system is somewhat flexible in how it integrates information from different modalities accommodating the inherent latencies for each sensory system and once the stimuli are presented outside of the window of integration they are perceived as information from separate events or stimuli. Spatial congruency is also an important factor and signals are not likely to be integrated if spatial discrepancies are large between the modalities (Ernst and Bülthoff 2004). The necessary temporal and spatial congruency for sensory integration is important as it allows for the perceptual system to differentiate between events that occur in our daily life. Thus, in order to integrate sensory information with the goal of improving perception and ultimately action temporal and spatial congruency is necessary. This again emphasises how the spatio-temporal properties of auditory and visual stimuli can greatly influence perception and indeed the integration of multisensory information.

2.1.3.1 Multisensory integration theories

2.1.3.1.1 The modality appropriateness hypothesis

In an attempt to explain how multisensory information is integrated, a theory or model is required in order to ground thinking and interpret results from research. The *modality appropriateness hypothesis* (MAH) is one such theory that attempts to account for the various findings from the perception literature relating to the integration of sensory information and it is particularly popular in the perception literature. This MAH assumes that each sensory modality, while being able to perform a series of functions, has one or two functions that it is particularly good at and even better than other modalities (Welch and Warren 1980). It states that vision dominates over audition for spatial tasks while the opposite is true for temporal tasks. Welch & Warren hypothesised that while vision dominates during spatial tasks, audition still possesses the ability to perceive properties relating to spatial information but with less acuity than vision. They argue the opposite for temporal tasks. Thus, this hypothesis helps to account for some of the illusionary effects that have been previously discussed in this section such as spatial and temporal ventriloquism. However, overall the hypothesis is somewhat rigid as the relative weighting of the different sensory modalities is not well accounted for. In the face of this rigidity, the *maximum likelihood estimation (MLE) model* is a more flexible framework, based on similar assumptions, providing not only an expansion of the *modality appropriateness hypothesis* but also a method of quantifying the multisensory interaction (Alais et al. 2010).

2.1.3.1.2 The maximum likelihood estimation model

In essence the MLE model is similar to the assumptions made by the modality appropriateness hypothesis since it predicts both spatial and temporal ventriloquism. However, the MLE model emphasises that in terms of integration the advantage of one modality over another is based on the reliability of the modality, rather than the modality itself. Ernst & Bülthoff (2004) highlighted this issue with the modality appropriateness hypothesis in relation to the terminology used. They pointed out that the use “modality appropriateness” was incorrect since the modality itself does not dominate rather it is the perception of this modality. More specifically, one should consider that the perceptual “estimate” of the modalities reliability dominates. Essentially the MLE model is a weighted linear sum that weights each modality involved in the integration according to their reliability, providing an optimal integration of the combined estimate with the lowest variance (Alais et al. 2010). Thus, when information from two different modalities are presented congruently the information is optimally integrated such that the variability of the combined estimate is lower than when they are presented separately (Wing et al. 2010), which is indicated with a bimodal benefit. However, when one modality is less reliable than another the weighting will shift towards the more reliable stimulus.

For example if visual and auditory information are presented with a spatial incongruency, the perceptual judgments will be more heavily weighted towards vision. In this context, vision is considered to be more reliable than audition for spatial information, as emphasised previously in this section. A similar, but reverse, scenario is predicted for a temporal task, where audition is weighted more favourably than vision when the stimuli are temporally incongruent. A second key element of the MLE model is that reliability is not fixed with each modality, it varies depending on how the stimulus is presented and picked up by the perceptual system. This implies a level of flexibility in the model, something that was missing from the modality appropriateness hypothesis, and is important since in daily life audio-visual information is perceived under different conditions and scenarios. The implication here is that a visual stimulus will not always be weighted more than an auditory stimulus as reliability is relative to the saliency of the individual stimuli.

The study by Alais & Burr (2004), as previously mentioned, provides evidence of optimal integration and importantly shows the effect that stimulus reliability can have on sensory weighting in perceptual integration. Their study investigated the effect of reducing the reliability of a visual blob by blurring it to various levels when it was presented in synchronization with an auditory stimulus. For the bimodal conditions participants were presented with two bimodal stimuli one after the other and had to judge which bimodal stimulus appeared more leftward. Importantly, for one of the presentations (either first or second) the audio-visual stimuli were spatially incongruent and the other presentation was congruent. Globally their results indicated that localisation errors were significantly better with the bimodal compared to unimodal conditions, supporting the MLE model by showing that audio-visual information can be combined by minimizing variance leading to the observed bimodal improvement. In relation to the reliability of the visual stimulus their results again supported the model showing that vision appeared to dominate the perceived position of the incongruent stimuli when this modality was reliable (low blur). When the reliability was slightly reduced for the visual modality (medium blur) participant's appeared to optimally integrate the audio-visual information, as predicted by the MLE model, and there was no bias towards either modality. More importantly, their results indicated a reverse ventriloquism effect when the visual stimulus was very unreliable (high blur). In this case there was a heavier weighting towards the auditory modality in perceiving the location of the incongruent stimulus since this modality was now more reliable than vision. This has important implications for sensory integration as it places an emphasis on the saliency of the stimulus or, in other words, on the reliability of the information perceived from the stimulus. Research using different modalities such as vision and proprioception have also provided strong support for this model (Ernst and Banks 2002). Whereas the *modality appropriateness hypothesis* provides a more black and white view towards the integration of audio-visual information in spatial and temporal tasks, the MLE model allows for a more flexible approach factoring in the reliability of the modalities in a weighted linear sum and importantly allows for these perceptual estimates to be quantified and tested.

2.1.3.1.3 Limitations of the maximum likelihood estimation model

While the MLE model represents an important step towards understanding how we integrate multisensory information the model is not a perfect prediction of reliability estimates by our perceptual system. A recent study by Gori et al. (2012) assessed the development of audio-visual integration using both temporal and spatial bisection tasks with children (ages ranging from 6-12 years) and adults. The bisection task involved both unimodal and bimodal conditions where a series of three stimuli were presented in sequence and participants were required to judge if the middle stimulus was closer in space or time to the first or third stimulus presented. For the spatial bisection task, multisensory stimuli was optimally integrated and resulted in improved precision for these conditions compared to the unisensory stimuli. However their results relating to a temporal bisection task indicated sub-optimal levels of integration as participants relied heavily on the auditory modality for this temporal task instead of integrating the available multisensory information. In this context the MLE model did not accurately predict sensory integration. These predictions would imply that, similar to the spatial task, audio-visual information would have been optimally integrated to improve perceptual precision. One possible explanation for these findings could relate to the high auditory tone used in the experiment. A study by Burr, Banks, & Morrone (2009) indicated that the MLE model predictions were better with low compared to high tones. These findings are supported by previous studies that have also found sub-optimal integration of audio-visual information for temporal judgment tasks (Burr, Banks, & Morrone, 2009; Shams, Kamitani, & Shimojo, 2000). The lack of support for the MLE model's predictions with temporal tasks indicates that this model has some limitations in terms of its ability to predict sensory integration in the temporal domain.

2.1.3.2 Multisensory integration: Stimulus saliency and congruency

Despite these contrasting findings for spatial and temporal tasks with the MLE model, it has been well established that in general spatially and temporally congruent audio-visual stimuli can enhance perception of multisensory stimuli over unisensory stimuli. Broadly speaking, the saliency of any given stimulus tends to influence the level of integration.

Bolognini, Leo, Passamonti, Stein, & Làdavas (2007) investigated the integration of audio-visual information with an auditory localisation task. Participants were instructed to judge the location of an auditory stimulus presented in one of several speakers and the visual stimulus was presented with varying saliency and spatial congruency. Their study firstly identified that with strong visual saliency and large spatial disparity there was a visual bias in localisations of auditory stimuli, indicating *spatial ventriloquism*. However, when the saliency of this visual stimulus was low and the modalities were spatially incongruent spatial ventriloquism disappeared. This provides strong support to the findings of Alais & Burr (2004) implying that the reliability or saliency of a given stimulus influences the sensory integration of two modalities. More importantly, regardless of visual saliency when this stimulus was spatially congruent with the auditory stimulus localisation accuracy increased significantly, indicating the integration of multisensory information. These results imply that in order for sensory information to be integrated the two modalities need to be spatially congruent and that once this is achieved the integration of the information significantly improves the perception of a given event. Indeed research on multisensory learning has found that training with congruent audio-visual stimuli significantly enhances performance in a visual motion detection task compared to training with incongruent audio-visual stimuli (Kim et al. 2008). While the previously discussed studies from Alais & Burr (2004) and Gori et al. (2012) presented both congruent and incongruent stimuli their overall results provided some support for Bolognini et al. (2007) as they indicated a bimodal benefit of multisensory conditions compared to the unisensory ones.

Other research has also provided support for this bimodal benefit using multisensory stimuli in a visual search task. One particular study coined a phenomenon known as the *pip and pop effect*, where an auditory stimulus, a pip, helps to improve the saliency of a visual stimulus making it seem to pop out of a background of several visual stimuli (Van der Burg et al. 2008). In this study participants were instructed to respond as quickly as possible to the orientation of a vertical or horizontal line segment, which was presented on a display with many oblique line segments with varying orientations. During this search task an auditory stimulus, with no information relating to the spatial location of the visual target, was played in synchrony with the visual target. The (correct) response times of participants were significantly improved when the auditory stimulus was present leading the authors to conclude that the presence of this auditory stimulus increased the saliency of the visual target resulting in the impression of this target popping out. Their overall results indicated that audio-visual binding took place during the experiment and that the high temporal saliency of auditory stimuli may have been a contributing factor for improving performance. Importantly, they also highlighted that this improved performance was not due to any alertness or cueing effect, which indicates that an auditory temporal stimulus can be integrated to improve performance even when it doesn't contain spatial information relating to a visual target. The lack of any spatial information in the auditory stimulus could have been an important factor since it was not spatially incongruent with the visual stimulus thus the two stimuli could be integrated and perceived as information from the same event.

Other studies have found improved speed and accuracy of reaction times when an auditory stimulus is congruently presented with a visual stimulus in space and time (Sinnett et al. 2008; Van Wanrooij et al. 2009). For example, Harrington & Peck (1998) found that while saccadic reaction times were significantly shorter for audio-visual compared to unisensory conditions, showing a bimodal benefit, the reaction times increased as the audio-visual stimuli were presented with greater spatial disparity. Overall, it appears that in order for multisensory integration to enhance performance, audio-visual stimuli need to be congruent in both space and time, although in certain circumstances an auditory stimulus with no spatial information can improve performance in a visual task.

The studies presented above indicate several important findings relating to the integration and perception of audio-visual stimuli. The MLE model has been employed in a lot of research studies as a method of both predicting and testing the integration of information from different sensory modalities. This model assumes that sensory information is combined in a statistically optimal fashion where each modality is weighted according to its reliability. The model predicts the dominance of visual and auditory information in specific conditions that involve spatial and temporal tasks, respectively and the studies presented above provide support for the model in this respect. When these studies presented audio-visual stimuli that are spatially incongruent, localisation of an auditory stimulus is biased in the direction of the visual stimulus indicating spatial ventriloquism. This effect highlights the high spatial saliency of the visual modality. In contrast, the opposite effect can be found for a temporal task. For example if an audio-visual stimulus is presented temporally incongruent with one another timing perception is biased towards the auditory stimulus indicating temporal ventriloquism. This highlights the high temporal acuity associated with the auditory modality. The MLE model implies that these effects occur due to the reliability of perceiving each modality in these different domains. Because of this emphasis on reliability of a given stimulus the model is quite flexible and even predicts a heavier weighting towards auditory information in a localisation task when a visual modality is blurred reducing its reliability. Importantly, when these modalities were congruent it enhanced the perception of a given event, in line with predictions from the MLE model.

While the perception literature discussed in this section provides a lot of information about how we perceive and integrate audio-visual information under different conditions it lacks some relevancy for real life. Perception, as highlighted earlier, is tightly coupled with action in our daily lives and the main role of perception is to inform our actions facilitating our interaction and connection with our environment. Thus, perception on its own is rare as we are constantly moving in our environment. In order to relate our perception to real life we must develop an understanding of how perception of different modalities impacts on our movements. The previous discussions surrounding perception will help inform the following section which will attempt to bridge the gap between perception and action. Thus, section 2.2 will discuss various studies that have assessed the coordination of movements in synchrony with visual and/or auditory stimuli.

2.2 Audio-visual stimuli and perception-action

2.2.1 Introduction to perception-action

As highlighted previously, perception research provides a strong base for understanding how we perceive sensory information but it is limited in that it does not address the consequences of perception on action. The use of perception-action paradigms often reveal more precise information relating to perceptual sensitivity than perception-only paradigms (Stoffregen et al. 2009). The following section will attempt to expand on these perceptual findings and will aim to examine research assessing the synchronization of movement with a variety of visual and auditory stimuli. Specifically, the discussion will aim to link these perceptual findings to the field of perception-action by investigating whether similar findings relating to modality bias and multisensory facilitation are found in these studies.

2.2.1.1 The ecological approach to perception-action

In the ecological approach to perception-action the individual and the environment are considered to be in constant interaction (Gibson, 1986). As a consequence of these interactions, the emerging motor behaviour can be analysed, for example, in terms of synchronization performance, i.e. the ability to move in relation to a specific external stimulus (see Section 2.2.2). Gibson viewed information as a central element in perception-action, implying that information constrains the movement behaviour. But it is not simply a one way process, Gibson's theory of ecological psychology highlights the relationship between perception and action as direct and cyclical (Williams et al. 1999) as he stated in his own words:

> "We must perceive in order to move and move in order to perceive"

This cyclical nature of the coupling implies that perception can influence action and in turn action influences perception. Thus, this approach implies that the task of the mover is to exploit physical (movement) and informational (environment) constraints to stabilise the intended behaviour. While these informational constraints can also come from within the individual themselves, for example through proprioception, in the context of this thesis a focus is placed on informational constraints from the environment. Depending on the nature of the task the solution may rely more or less on physical or informational regularities (Warren 2006). Bringing focus back to the original discussion surrounding the importance of knowing what and how information is used; in order to understand this coupling between perception and action the ecological approach aims at identifying what information from a stimulus is relevant for action and how this information is used to control action (Sternad 2009). This thesis will focus on these two aims by manipulating the informational constraints placed on action and assessing the consequences of these different constraints. While the ecological approach provides the foundations for understanding the coupling between perception and action, the dynamical systems approach builds on this line of thought and provides a strong quantitative means of testing the perception-action research assumptions.

2.2.1.2 The dynamical systems approach to perception-action

2.2.1.2.1 An introduction dynamical systems theory

The dynamical systems theory is closely related to the field of ecological psychology. This approach views perception-action as a complex system whose behaviour is best understood at a macroscopic level where the individual elements of the system combine to form patterns (Williams et al. 1999). A key feature of this theory is the concept of self-organisation whereby a system organises itself spontaneously without any specific agent (e.g. a brain) “telling” the system what to do (Kelso, 1995). In the case of human movement, physical (mechanical aspects of movement) or informational (stimuli from environment) constraints influence the overall system causing it to evolve between different organisational states. This is in essence the concept of self-organisation. In other words the interactions between the various elements of the system (i.e. the individual and the environment) emerge based on the constraints placed on the system. Importantly, this approach places a strong emphasis on the role of information within a system since the coupling between the interacting parts of a system is described as informational and even the variables used to quantify this interaction are based on capturing this informational coupling (Kelso 1995). A link between Gibson's ecological approach and dynamical systems exists here since both approaches view the interaction between the parts of a system as a consequence of the constraints placed on that same system. Both also place an important emphasis on information and its role in constraining the system and ultimately producing behaviour. Additionally, the two approaches see coordination as a temporary (spontaneous) formation to complete a given task, for this reason information is considered to be meaningful and specific to the dynamic patterns that human movement systems create (Kelso 1995).

Kelso's early work from the 1980's on applying the dynamical systems approach to human movement (Kelso, Holt, Rubin, & Kugler, 1981; Kelso, 1984) established that simple motor coordinated actions such as wrist or finger oscillations displayed features of a complex dynamical system. Using the relative phasing between two wrists/fingers as a way of quantifying the interaction (i.e. relative phase was an order parameter[1]), even though the available degrees of freedom would suggest that a large number of states would be available to the system, only two stable states were observed. These two stable states occurred when the two fingers/wrists were moving in the same direction (in-phase) and when they moved in the opposite direction to each other (anti-phase) and these stable states represent an important feature of dynamical systems. In-phase is typically more stable than anti-phase and while other states are possible they feature a significantly higher amount of variability and require learning in order to become stable (Kelso 1984). Kelso also established that the frequency of oscillation was the control parameter[1], which caused phase transitions from anti-phase to in-phase as the frequency was increased beyond a critical point. However, when the frequency was reduced following the transition subjects remained at in-phase highlighting that this state was more stable than anti-phase. Subsequently, these findings were formalised with the HKB model (Haken et al. 1985) providing an opportunity to test the dynamical systems perspective through

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[1] A control parameter, such as frequency in human movement systems, can bring a system from one state to another while an order parameter, such as relative phase between two limbs in movement systems, quantifies these changes that occur.

experimentation. With this model researchers could begin to test whether these features of a dynamical system were present in other circumstances and environments other than an oscillating finger/wrist task.

These essential features have been shown across a variety of different environmental settings where researchers have manipulated the type of perceptual information and/or movements such as coordinating both arms and legs (Kelso and Jeka 1992), and coordination of limbs between persons (Schmidt et al. 1990). The latter study had significant importance in terms of expanding the support for the dynamical systems approach to coordination for movement between-persons. They showed that the coordination of limb movements between two people was achieved using only visual information of the other person's movements. More importantly, this coupling could be explained using the dynamical systems approach as their results indicated the same key features of a dynamical system as found in Kelso's early work in the 1980's: switching between states under certain conditions and the existence of only two stable states (in-phase and anti-phase).

2.2.1.2.2 The interplay between absolute and relative coordination

Broadly speaking the type of coordination can be broken up into two different categories, relative and absolute coordination. Absolute coordination is evidenced when the phase relationships, e.g. between an individual's movement and that of a stimulus, are constant, otherwise known as phase locking (Kelso 1995). On the other hand for relative coordination no phase locking is present, instead the entrainment varies constantly (Issartel et al. 2007) indicating a much weaker level of coordination. The number of constraints placed on the system can influence the type of emerging coordination. For example a study by Richardson, Marsh, Isenhower, Goodman, & Schmidt (2007) assessed the intentional (absolute) and unintentional (relative) coordination between two people rocking in chairs. In relation to the unintentional element of their study, subjects were required to rock their chair rhythmically, ignoring the other subject, under different viewing conditions (no view of other subject, focal view and peripheral view). For their unintentional conditions due to the low number of constraints placed on the participants (i.e. they could rock at their own pace) the results indicated the presence of relative coordination when the subjects focused on the other person (focal view). Importantly these results provided further support for the dynamical systems approach to human movement, specifically interpersonal coordination, and highlighted how the coupling in perception-action has a more informational than physical basis (Richardson et al. 2007).

Schmidt et al. (1990) assessed the intentional coordination of leg oscillations between people, which is an example of absolute coordination. In this study participants were instructed to coordinate the oscillation of their leg with that of another person sitting beside them across various experimental conditions that involved the manipulation of the frequency of oscillation. In this study more constraints were placed on the participants since they were not free to oscillate/move their legs at their own pace. Instead they intentionally had to coordinate their movements with another person. As a result of these additional constraints the participants in this study were able to maintain the same frequency of oscillation during the experiment indicating the presence of absolute coordination.

Thus, any modifications of the constraints on either the participant or the stimulus, for example the removal of key trajectory information, will result in changes in the motor behaviour. Based on this rationale, this thesis will investigate the type of information utilised in perception-action coupling by focusing on absolute coordination between different environmental stimuli and an oscillatory movement. This thesis will also focus on exploring the specific role of information in stabilising coordination. Modifying specific perceptual features of different stimuli and assessing the changes that occur in terms of behaviour can help in highlighting the role of this information in a perception-action task.

2.2.2 Sensorimotor synchronization

In order to quantify the dynamics of coordination in human movement, the motor behaviour is often described in terms of synchronization. Pikovsky, Rosenblum, & Kurths (2003) define synchronization as the adjustment of rhythms due to an interaction. This interaction can be weak, as with relative coordination, or strong, as with absolute coordination. Essentially, synchronization is a way of quantifying the coordination dynamics and is ubiquitous in nature covering a variety of different interactions from within to between people, as previously highlighted. In light of the broad number of interactions that can be described in terms of synchronization a more specific definition is required for clarification purposes. Repp & Su (2013) called *Sensorimotor Synchronization* "the coordination of rhythmic movement with an external rhythm, ranging from finger tapping in time with a metronome to musical ensemble performance". Thus, sensorimotor synchronization is a measure of the behavioural output of an interaction between a participant's movement and an external stimulus. This definition limits the concept of synchronization to external rhythms but is suitable in the context of this thesis since only this type of synchronization task will be addressed.

External rhythms are ubiquitous in daily life and as highlighted previously developing an understanding of how these external rhythms are perceived and used to support action is one of the main aims of ecological psychology and dynamical systems theory. The use of external stimuli in the assessment of sensorimotor synchronization allows for research to explore these questions and gain insight into how we interact with our environment. This can be achieved by modifying an external stimulus in a specific way (for example changing the continuity of a stimulus) and examining the impact that this change has on sensorimotor synchronization. Researchers in perception-action have employed this paradigm extensively in order to develop an understanding of how we synchronize our actions with auditory and visual information.

2.2.2.1 Variability in synchronization

Inherent to the synchronization process and at the very heart of self-organised behaviour is the concept of dynamic instability (Kelso et al. 1990; Kelso 1995) which can be quantified as variation of a specified order parameter of the system. This variability is a natural characteristic of organisms and helps to reveal the underlying dynamics of motor control (Newell and Slifkin 1998). An important consideration when assessing the role of variability in motor coordination is that it must be viewed with respect to the type of movement that is being analysed (Piek 2002) since variability has been used as a method of answering many different research questions (Müller and Sternad 2009). Thus, depending on the context variability can be seen as either a negative or a positive feature in motor control.

2.2.2.1.1 Different views of variability

Variability in behaviour is a source of information that helps in understanding the underlying dynamics of a system (Oullier et al. 2006). Kelso's early work from the 1980's utilised measurements of variability in finger and wrist oscillations to demonstrate that these systems contained key features of a dynamical system (Kelso et al. 1981; Kelso 1984). Importantly, through this work they highlighted that synchronization becomes significantly more variable, i.e. a loss of stability, in the anti-phase mode as the frequency of oscillation is increased and at a critical frequency a switch to the in-phase mode occurs. This instability is considered a mechanism through which a system transitions from one stable state to another (Kelso 1995) and in this case the system remained stable by adapting to the frequency changes. Rather than trying to avoid the instability of motion in a system, as scientists usually try to do, the dynamical systems approach embraces it as a fundamental mechanism of self-organisation (Kelso 1995). Therefore, variability as a method of quantifying the stability of a system is a critical aspect for dynamical systems analysis (Hamill et al. 2000) and serves to highlight the ability of a system to adapt to changes.

The very idea of survival in a dynamic environment requires this kind of adaptation and flexibility that has been described. Indeed, complex systems seem to live near instabilities in order to be able to express a type of flexibility and adaptability that is central to all living organisms (Kelso 1995). Take for example an elite athlete performing the long jump. During the run up an athlete may need to make slight adjustments in order to maximise their performance and eliminate errors that have accrued (Lee et al. 1982) and variability, in the form of a compensation during run up, may allow for these functional on-line adjustments in the athletes stride pattern to be made (Williams et al. 1999). While generally low variability is observed in skilled behaviour performed with a high level of proficiency (Piek 2002; Müller and Sternad 2009) the ability to adapt to changes in a competitive environment necessitates some variability when needed.

As previously mentioned variability can be used as a measure of the strength, or stability, of a particular emerging behaviour in a system where less variability indicates a more stable behaviour and vice versa (Piek 2002). Here, we see how variability, as a specific order parameter, can be used to characterise the stability of the system when the objective of the task is to synchronize movements with an external stimulus. Within this context, the variability of a specified order parameter provides insight into the stability of the system. Along these lines, changes in stability provide an insight into the role and nature of the perception-action coupling with these stimuli. The variability of the behaviour will be analysed in this thesis with a specific focus on two types of external stimuli: auditory and visual. The quantification of this variability requires specific methods that will be discussed in the following section.

2.2.2.2.2 How variability is assessed

There are a huge variety of ways to quantify variability of a given system. Depending on the type of task used and indeed the research questions that are being investigated different methods of assessing variability may be more appropriate than others. In light of the complexity and variety in assessing variability the purpose of this section is to highlight the specific variables that are most appropriate for the task and research questions in this thesis while providing a justification for their use in this context. One of the most common methods of quantifying the behaviour of a system is by looking at the phase relationship between components of the given system. In the case of synchronization with external stimuli this phase relationship typically stems from the time series created by the external stimulus and the movements of the person. The phase relationship of the system can be determined with the variable *relative phase* which is a measure of the interaction or coordination between two time series (Stergiou 2004). Relative phase essentially captures the emerging patterns of the system describing the interaction in terms of degrees. 0° corresponds to perfect synchronization between the two time series, in-phase, while 180° represents the time series moving opposite to each other, anti-phase. Relative phase is particularly useful and popular in the literature since it compresses four variables (displacement and velocity of two time series) into one measure (Stergiou 2004). It can be calculated in various ways and these different methods are used in relation to the type of movement or task in a given experiment.

This relative phase can be expressed in a continuous or discrete format. Discrete relative phase assesses the phase relationship of the two time series at the local maximum and minimum points of movement (Stergiou 2004). While some researches have shown that discrete measures of relative phase are sufficient for representing the dynamics of some movements (Kelso 1995) others have argued that further support for these claims are needed (Stergiou 2004). While analysis of these discrete points can contain information about the dynamics of the system (Stergiou 2004) continuous relative phase utilises every sample of data and captures the complete picture of the phase relationship between the movement and the stimulus. For this reason, it is typically used in the literature but ultimately this decision is dictated by type of movement and the research questions. For example, analysing movements such as flexing the index finger on the beat of a metronome discrete relative phase may be sufficient for examining the underlying dynamics of the system given the discontinuous nature of the movement itself. In contrast to this other movements such as postural sway or the swinging of a handheld pendulum may require an analysis of continuous relative phase as the movement between the endpoints may also be important for motor control.

2.2.2.2.2.1 Relative phase calculation: A classic method

The most common method of calculating relative phase involves calculating the phase angles of the two time series and subtracting these phase angles from each other. In order to calculate the required phase angles of the time series the equation below is used:

$$\theta_i = \arctan(\dot{x}_i / x_i),$$

where $\dot{x}_i$ is the normalised angular velocity of the i^{th} data point and x_i is the angular displacement of the i^{th} data point. Relative phase is then calculated by subtracting these phase angles from each other. The normalisation of angular velocity can be an issue for certain types of data, for example with time series that have fluctuations in frequency throughout, and there are multiple ways to normalise the velocity. In the experiments presented in this thesis synchronization with the external stimulus is intentional and frequency fluctuations are minimal thus this issue of velocity normalisation does not greatly affect the data. For a detailed discussion on the effect of different normalisations of velocity in the computation of relative phase see Varlet & Richardson (2011).

2.2.2.2.2.2 Relative phase calculation: The Hilbert transform

As mentioned previously there are multiple methods of calculating relative phase. Another popular calculation of relative phase is through the *Hilbert Transform* which has been used widely in the literature (Teplan et al. 2009; Richardson et al. 2009; Varlet et al. 2012). This method of calculating relative phase is derived from the concept of the analytic signal which is used in mechanical engineering to identify elastic and dampening properties of a vibrating system, meaning that this method is particularly suited for nonstationary data (Pikovsky et al. 2003). The continuous phase angles are computed using:

$$\phi(t) = \arctan\left(\frac{s(t)}{Hs(t)}\right)$$

where s(t) and Hs(t) are the real and imaginary parts of the analytic signal, respectively. Due to distortions created during the Hilbert transform the first and last cycles are typically removed (Pikovsky et al. 2003). Overall this method of calculating relative phase is quite robust in that it avoids magnifying any noise in the data due to the fact that no derivatives are used in the calculation and it can handle signals that are nonstationary and nonsinusoidal (Robertson et al. 2013). All computations of relative phase in this thesis utilised this method.

2.2.2.2.2.3 Standard deviation of relative phase

The main function of relative phase is to aid in describing the pattern of coordination between movement and an external stimulus. Another important characteristic of the relative phase is the stability of the variable over time or at a specific location in the movement. This can be quantified using the standard deviation (SD) of relative phase. For example, a participant may have a relative phase value close to 0° but the SD of relative phase may be very high. This would indicate that while the participant was able to move in phase the stability of the coordination was quite poor and, in the context of synchronization with external stimuli, may indicate a high level of task difficulty or issues relating to the perception of the external stimulus. Regardless of the underlying process creating the variability this example highlights the importance of viewing both the relative phase and the SD of relative phase values in order to see both the general pattern of coordination and the stability of this pattern. As highlighted previously stability is a central feature in the dynamical systems approach and should not be overlooked during analysis.

2.2.3 Task complexity and the application of research findings

A common question in perception-action research relates to the application of a particular study to “real-life”. Broadly speaking depending on the type of task chosen the results of a particular study can have different outcomes in terms of how they impact on “real-life”. In this light research can be generally broken up into two different categories, those using simple movements or tasks and those using more complex movements or tasks. Both of these types of tasks can have applications in the real world however typically this application occurs at different levels.

Research using simple tasks within the field of perception-action is mainly aimed at exploring the fundamental principals that govern our interaction with our environment. By their very nature these simple tasks have a small number of degrees of freedom and allow researcher to examine how small changes to the type of information provided to a participant influence the perception-action cycling in terms of synchronization performance. For example, it has been shown that synchronization of simple pendulum movements through the wrist is significantly better with a short auditory beep compared with a short visual flash (Varlet et al. 2012). By using this simple task the conditions can be tightly controlled meaning that very few other factors have a significant impact on the synchronization other than the manipulations made by the researcher, in this case changing the modality of the stimulus from auditory to visual. This type of controlled and simple experimental design allows for researchers to then infer from the synchronization results how we process different types of information, which is extremely useful in order to develop a fundamental theory of how perception-action coupling occurs in humans. Yet, the disadvantage with using simple tasks is that they are generally not "ecological" or related to real life in terms of both the type of task and the stimulus used. Thus, the ability to directly apply research findings using simple tasks to real life is limited. Instead this direct application research using simple tasks serve to add provide a fundamental basis for understanding how we perceive and act, which can be built on in order to generalise these basic principals to more complex or "ecological" tasks.

Indeed, this has been the approach adopted by researchers employing dynamical systems theory to the understanding of perception-action coupling. Kelso's early work focused on simple tasks such as finger and wrist movements (Kelso, Holt, Rubin, & Kugler, 1981; Kelso, 1984). The general characteristics of a dynamical system that were established with these simple tasks have since been found in more complex movements such as multi-limb coordination (Kelso and Jeka 1992) and even in the coordination of limbs between two people (Schmidt et al. 1990). Research has even begun to employ dynamical systems theory in order to understand the interaction between an attacker and a defender in soccer (Duarte et al. 2012), which is an extremely ecological experimental situation. The development of this theory from simple tasks to more complex movements and interactions highlights how research examining simple tasks can be useful in terms of establishing a general theory about how perception-action coupling is controlled for both simple and more complex tasks. However it is important to note that the generalisation of basic principals found with simple tasks to more complex tasks does not always work.

In a review of literature surrounding motor learning with simple and complex skills the authors noted that in relation to feedback and physical guidance the principals developed with simple skills cannot be generalised to complex skills and that certain variables that are used to enhance simple skill learning are detrimental to the learning of complex skills (Wulf and Shea 2002). Importantly, the authors also highlighted that if research is aiming to be directly applied to an ecological or real life setting than complex skills need to be utilised (Wulf and Shea 2002).

This highlights the main difference between the use of simple and complex tasks in perception-action research, the former focuses mainly on a fundamental understating of how we perceive and act at a very basic level while the latter typically focuses on how the findings may aid real life applications. The important work by Goode & Magill (1986) on motor skill learning with badminton serves highlighted the direct application of using complex skills. The focus of this study was to establish how different structures of training badminton serves would influence motor skill learning. Their results indicated that performance in retention and transfer tests were significantly better with the random practice schedule group compared to a block practice schedule group. Given the complexity of the skill and the fact that an ecological setting was used, these results could easily be directly applied to badminton serve training in real life. The use of simple and complex tasks each serve their own purpose in terms of enhancing our understanding of our interactions with the environment, the former focusing on a basic understanding of how we perceive and act and the latter focusing on applying the findings to real life. The focus of this thesis is on the former and aims at developing a basic understanding of how we perceive auditory and visual information from our environment and how these perceptions impact on performing a simple synchronization task.

2.2.4 The importance of spatial and temporal information

The detection of change in the environment is an essential feature of an animal's survival and since these changes can be detected through space and time, these spatio-temporal events are very important for perception-action. Therefore understanding the role of spatial and temporal information in synchronization is an important question. The earlier discussion surrounding the perception of auditory and visual stimuli highlighted that spatial and temporal information are perceived in different ways for auditory and visual stimuli. Namely, visual stimuli are quite salient when spatial features are available while auditory stimuli show strong saliency when temporal features are available. The following section will attempt to expand on these perceptual differences by discussing the synchronization of movements with auditory and visual stimuli with varying spatial and temporal structures. The first part will discuss synchronization with auditory and visual stimuli that contain only temporal information while the second part will discuss synchronization when the two modalities contain both spatial and temporal information[2].

2.2.4.2 Synchronization with temporal stimuli

2.2.4.2.1 The case for auditory temporal stimuli

As highlighted earlier in this thesis auditory stimuli are more temporally salient compared to visual stimuli, which is demonstrated with the temporal ventriloquism effect where a sound can capture the timing of a visual stimulus. This high saliency of auditory stimuli within the temporal domain had a strong influence in the tapping literature specifically (Repp 2005). A useful way to understand how sensory information is integrated in movement production is to assess the direction of the synchronization. This can be established through a variety of different variables capturing the arrival of the participant's movement at a given end point in relation to that of the stimulus. A variable commonly used is called *asynchrony*, which is the time difference between the tap and the presentation of a stimulus. It is important to note that the stimuli can have different properties. They may be 1) continuous, such as a tone that is frequency modulated between a low pitch and a high pitch or 2) discrete, where a series of short beeps are presented in sequence with a set interval between each presentation. The latter stimulus is heavily used in the tapping literature. The emerging movement pattern where taps typically precede the auditory stimulus by a

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[2] While it would be advantageous to assess the spatial and temporal aspects of stimuli separately, it is impossible to represent a stimulus with only spatial information since temporal information is inherent in the very analysis of synchronization and present in all events regardless of sensory modality (Repp and Penel 2002).

few tens of milliseconds is known as *Negative Mean Asynchrony (NMA)* (Aschersleben 2002; Repp 2005). This NMA indicates that participants tend to over anticipate, instead of simply reacting to, the occurrence of a stimulus, yet with practice and learning NMA can be reduced and it is frequent to observe that NMA is less variable in musicians (Summers et al. 1993; Repp 1999; Repp and Doggett 2007; Fujii et al. 2011; Boasson and Granot 2012).

This tendency for participants to precede a discrete auditory stimulus is not limited to a finger-tapping task and has also been supported with other closely related tasks. For example, Elliott et al. (2009) used three different tapping tasks: 1) the typically used discrete tap, 2) a continuous action where contact with a sensor is maintained while applying a force in a sinusoidal fashion and 3) a pulsed action that was intermediate between the two other tasks where force was applied abruptly. For all of these tasks participants tended to precede the stimuli as well. However, other studies using a wrist pendulum task have found that participants tend to follow discrete auditory stimuli (Varlet et al. 2012) which indicates that the continuity of the task may modulate the dynamics of the coordination resulting in differences in leading and following the stimulus. Importantly, it has been highlighted that discrete and continuous tasks constitute different synchronization processes for timing movement with stimuli. For discrete tasks timing appears to be controlled on a sequential cycle-to-cycle basis using linear error correction and in contrast for continuous tasks timing is controlled through continuous within-cycle corrections using a driven oscillator framework (Torre and Balasubramaniam 2009). The use of sequential versus within-cycle organisation of timing more than likely explains the differences between the studies discussed above.

2.2.4.2.2 The case for visual temporal stimuli

Due to the dominance of auditory stimuli in the temporal domain much less focus has been placed on discrete visual stimuli that contain solely temporal information. Studies assessing finger tapping with discrete stimuli found better levels of synchronization with auditory compared to visual stimuli (Repp 2005; Repp and Su 2013), which provides support for the perceptual findings relating to the high temporal saliency of auditory stimuli. Repp & Penel (2002) attempted to bridge the gap between the perception and perception-action literature by assessing the well know perceptual dominance of audition over vision in the case of temporal information in a sensorimotor synchronization task. Their research represented a novel exploration of sensorimotor synchronization with auditory and visual rhythms. In one experiment, participants synchronized the tapping of their index finger with a discrete auditory and a visual stimulus, presented in unimodal conditions. The auditory stimuli consisted of a synthetic piano note, C8 (4186 Hz), while for the visual stimuli two sets of participants were tested each with a different stimulus. The first consisted of an "X" that transitioned from a frame on the left to the right of the screen signifying an event while the second stimulus was the flash of a LED. Participants were required to tap in time with the stimulus and also to report any time-shift events. These time-shifts are known as *Event-Onset Shifts (EOS)* where during the presentation of a discrete rhythmic stimulus one presentation is displayed ±100 ms from the expected onset causing participants to perform a *Phase Correction Response (PCR)*. The results indicated that in terms of variability of the asynchronies clearly showed a significantly better performance with the auditory (16.2 ms) compared to the visual (25.6 ms) stimulus (58% increase in variability) regardless of the type of visual stimulus. Elliott, Wing, & Welchman, (2010) also found that for two reliable metronomes asynchrony variability in finger taps was significantly higher for the visual (48 ms) compared to auditory (27 ms) metronome (77% increase in variability). Subsequent studies have also found evidence of this auditory dominance over visual stimuli for discrete temporal stimuli (Chen, Repp, & Patel, 2002; Hove, Spivey, & Krumhansl, 2010; Jäncke, Loose, Lutz, Specht, & Shah, 2000; Repp & Penel, 2004; Varlet et al., 2012).

2.2.4.2.3 A comparison between discrete and continuous stimuli

The findings discussed above relate only to discrete stimuli. Significant changes occur to the structure of synchronization when the continuity of the stimulus is modified. A study that assessed finger-tapping seemed to indicate that while response times were generally similar, higher variability in taps (measured as standard error of the mean response time) were observed with continuous (7.7 ms) compared to discrete (3.2 ms) sounds (140% increase in variability) (McAnally 2002), although this was not specifically compared in their results and the type of auditory stimulus used may have been problematic (Rodger and Craig 2011). In an attempt to understand if more information provided between beats can help to stabilise coordination Patel et al. (2005) assessed finger-tapping synchronization with different types of auditory stimuli with varying event rates. They found that as the event rate (the number of additional sounds between two synchronization points) increased the asynchrony became less negative, approximately 40 ms asynchrony for highest event onset condition and 80 ms for lowest event onset (asynchrony increase of 100% between highest to lowest event onset). While these subdivided stimuli with increased event rates were not continuous per se they did provided additional information between taps that seems to improve the synchronization. Varlet et al. (2012) found no significant differences in variability of relative phase between their discrete and continuous auditory stimuli with a wrist pendulum task (both approximately 23° SD relative phase). Due to the limited number of studies directly comparing discrete and continuous auditory stimuli, the exact effect of continuity for this modality remains unclear and requires further investigation.

The use of continuous temporal visual stimuli is quite rare in the synchronization literature and differences in tasks employed to investigate these stimuli make comparisons difficult. While it has been stated that in general synchronization with auditory compared to visual stimuli is better, more recent research has presented some contrasting findings. A recent study by Varlet et al. (2012) compared synchronization performance with auditory and visual stimuli presented either discretely or continuously. The discrete auditory stimulus (discrete beep, approx. 19° mean relative phase) compared to the discrete visual stimulus (discrete flash, approx. 29° mean relative phase) had better levels of synchronization (increase of 52% in relative phase with visual stimulus), which is in line with previous research (e.g. Chen et al. 2002; Elliott et al. 2010). However, when both modalities were continuous the difference between the auditory (frequency modulated tone, approx. -21° mean relative phase) and visual (square fading between a black and red colour, approx. -20° mean relative phase) stimuli disappeared. This implies that the visual modality may be better suited to continuous information compared to the auditory modality. Saliency issues may have contributed to the lack of differences between these continuous stimuli since the synchronization point for the auditory stimulus was the high pitch which is known to be quite salient in a frequency modulated tone while in comparison the red endpoint for visual condition may not have been as salient. Interestingly there were no significant differences found between the discrete auditory and continuous visual conditions.

A study by Hove et al. (2010) also assessed the impact of continuity on synchronization performance. In their study they only modified the continuity of the visual stimulus and compared these modifications to a discrete auditory stimulus with a finger-tapping task. All stimuli were presented in unimodal conditions and when these stimuli were discrete audition (average 90% successful trials) was superior compared to vision (average 35% successful trials) representing approximately a 157% increase in successful trials with audition. However, when the visual stimulus was presented as a continuously fading square with appearing and disappearing snowflakes (average 30% successful trials) synchronization was still better with the discrete auditory stimulus, again representing over a 150% increase with the auditory condition. The use of different tasks in these two studies may help explain the contrasting results relating to the use of continuous visual stimuli. It has also been shown that the continuity of the task can affect the dynamics of coordination. Discontinuous movements such as tapping may be better at error correction than continuous movements (Elliott et al., 2009) which may explain the differences discussed above.

While the literature sometimes presents contrasting findings relating to the ability to synchronize with discrete and continuous stimuli it is important to highlight the possible theoretical basis for understanding the differences between these types of information. Firstly it must be noted that the type of synchronization task that is performed can significantly influence the mechanisms used for the temporal control of movement. As mentioned previously the mechanism for timing discrete tasks relates to linear error correction where a sequential cycle-to-cycle basis is used to control movement (Torre and Balasubramaniam 2009). For this particular mechanism of temporal control a person tapping their finger in time with a discrete auditory metronome adjusts each tap based on the perceived asynchrony from the previous tap. Other explanations for the discrete control of movement relate more to the information provided by the stimulus rather than the nature of the task itself. In the particular example above there is a temporal void between each onset of a beat, in other words the person has no information between each beat. The question raised here is how this temporal void is "filled" by the person in order to ensure that their movement are closely synchronized with the onset of the next beat. Thus, it has been hypothesised that based on this discrete onset of information some internal mechanism must exist that allows a person to prospectively guide and control movement (Craig et al. 2005). This mechanism acts as internal temporal information that helps a person accurately anticipate the next onset of a beat, which is reflected in the typical anticipatory arrival of a finger tap when it is being synchronized with a discrete auditory metronome. It is also important to highlight that this internal mechanism is limited in that beyond an inter-beat-interval of around 2.5 sec synchronization, or rather the ability to predict the onset of the next beat, becomes much more difficult (Craig et al. 2005).

In contrast with this for continuous tasks timing is controlled through continuous within-cycle corrections using a driven oscillator framework (Torre and Balasubramaniam 2009). Thus, a continuous movement coupled with a continuous stimulus appears to be corrected on a continuous basis and does not rely on an internal anticipatory mechanism to "fill-in" for any temporal void, since no such void exists with this type of information. The obvious advantage here is that the synchronization between the movement and the stimulus is continuous updated and thus may be more reliable than synchronizing with discrete stimuli. Some evidence exists from the literature that appears to support the idea that continuous information can help to improve synchronization compared to discrete information. For example, the work by Patel et al. (2005), which was discussed above, appears to indicate that as the amount of information between two synchronization points is increased the typical negative asynchrony becomes less and less indicating better synchronization performance. Thus, it would appear that the information provide in the "temporal void" between two beats can be coupled to the overall movement resulting in improved performance. Another example can be found from (Rodger and Craig 2011) which specifically aimed at filling-in this temporal void with continuous information. In their study, participants synchronized finger movements between two barriers with discrete and continuous auditory stimuli. Again, their results appeared to indicate that the information provided between two discrete points significantly improved the stability of synchronization providing further support for the benefits of continuous information in synchronization tasks (approx. 20% decrease in SD of error with continuous condition). However, due to the lack of studies directly assessing differences in synchronizing with discrete and continuous information further research may be needed in this area.

2.2.4.2.4 Specific Characteristics of auditory stimuli

The use of continuous auditory stimuli in the synchronization literature tends to take the form of a frequency-modulated tone that moves from a low to a high pitch sinusodially. An interesting phenomenon occurs in synchronization with this type of stimulus where discrimination and synchronization is better with the frequency peaks (high pitch) compared to the troughs (low pitch) (Demany and McAnally 1994; Cheveigné 2000; McAnally 2002). In these studies the phenomenon was reported across a wide variety of frequency ranges and is still present even when researchers attempted the improve the saliency of the trough by introducing an amplitude modification to the signal (Demany and McAnally 1994). This phenomenon has important implications for the study of synchronization since it implies a given bias towards one endpoint of the stimulus. This bias could alter the dynamics of coordination and should be considered as a key factor when interpreting results. Importantly, Varlet et al. (2012) gave instructions for participants to synchronize the maximal adduction of the wrist pendulum with the peak (high pitch) of the continuous auditory stimulus and in their analysis they calculated discrete relative phase using this synchronization point. Due to the fact that these instructions would have already placed a bias towards the high pitch and since their analysis only used one endpoint, the synchronization point, it is impossible to determine if the auditory bias towards the high pitch was present in this study. However, it can only be presumed that the same bias may have been present and that the use of the high pitch as the synchronization point may have aided the saliency of the auditory stimulus for their task.

Overall, auditory stimuli appear to dominate over visual stimuli when they are presented discretely. However, when the stimuli are presented continuously there are contrasting findings. Issues relating to the saliency of the stimuli used in these studies may have impacted on the results. Firstly, for auditory stimuli that are presented as frequency modulated tones, the high pitch is more salient compared to the low pitch, which could improve synchronization at this particular point in the task. In contrast to this, little is know about the saliency of the two endpoints of a continuous temporal visual stimulus such as a stationary square that changes in colour. One of the aims of this thesis will be to address these questions by comparing continuous visual and auditory stimuli that contain only temporal information. As highlighted previously, differences in the type of tasks used in studies can be a major issue for comparing results. In light of these difficulties, this thesis will use wrist-pendulum based task, which is similar to the task used by Varlet et al., (2012). This will facilitate later comparisons between these two studies.

2.2.4.3 Synchronization with spatio-temporal stimuli

Spatio-temporal stimuli closely relate to how we perceive stimuli in daily life since space and time are intertwined (Nijhawan and Khurana 2010). In contrast to the previous section where the focus was essentially on temporal discrete stimuli, this section will concentrate on studies assessing synchronization using stimuli containing both temporal and spatial information.

2.2.4.3.1 The case for visual spatio-temporal stimuli

One study aimed to fill in the gap in the literature by comparing discrete and continuous visual stimuli that contained spatio-temporal information (Buekers et al. 2000). Participants were required to synchronize (in-phase and anti-phase) movements of their forearm with two different visual conditions presented on a LED runway, continuous and intermittent (appearance only at reversal points). In general arm movements followed the intermittent condition and preceded the continuous conditions, which is in direct contrast with the tendency for participants to precede both discrete and continuous temporal stimuli in finger-tapping tasks (see Hove et al., 2010). Since Varlet et al. (2012) found the same results as Buekers and colleagues it would appear that the continuity of the task itself has an impact of the tendency for participants to precede or follow a given stimulus.

In relation to the stability of coordination, the results clearly indicated that participants had significantly better performance with the continuous compared to the intermittent conditions and with in-phase compared to anti-phase. The authors suggested that the results pertaining to the intermittent stimulus occurred due to a weakening of the perception-action coupling since less information was available. However it is important to note that in the intermittent condition synchronization was still possible even though the perception-action coupling was weaker which implies that the information at the endpoints of the stimulus provide key information that is essential for stabilising coordination. The importance of the endpoints of a visual stimulus was again made by Hajnal et al. (2009) who found that coordination was significantly reduced, although still possible, when the endpoints of a visual stimulus were no longer visible (average of 17% increase in variability when endpoints were occluded compared to other occlusion locations). Both of these studies seem to indicate that the information provided at the endpoints of an oscillating spatio-temporal visual stimulus is important and overall the information between these endpoints helps to significantly improve synchronization.

2.2.4.3.2 The case for auditory spatio-temporal stimuli

Similar to visual stimuli, discrete auditory stimuli that contain spatial information are also uncommon in the literature. A recent study by Rodger & Craig (2011) was conducted in a similar vain as Buekers and colleagues but focused on auditory stimuli instead of visual. In this study, participants were required to synchronize finger movements between two barriers with continuous and discrete auditory stimuli that contained spatial information in the form of the sound panning between the left and right ears of the headphones. Their results indicated that while there was no differences in synchronization performance there was reduced variability for the continuous compared to the discrete conditions (approx. 20% decrease in SD of error with continuous condition). Other research has found some contrasting results using similar stimuli such as a study by McAnally (2002) that found greater variability with their continuous compared to discrete auditory stimuli (140% increase in variability). As highlighted by Rodger & Craig (2011), the differences between these results could be due to the nature of the auditory stimuli used by McAnally (short interval durations and a frequency-modulated tone). Additionally, the differences in tasks may have also contributed to these contrasting results since McAnally used a discontinuous tapping task while Rodger and Craig (2011) used continuous finger movements between two barriers. Their results also supported the previously discussed findings relating to the arrival of movements at endpoints with continuous stimuli, thus, it seems plausible that the continuity of the task can have a significant impact on the coordination dynamics.

When spatial and temporal information are available for either auditory or visual stimuli it seems to improve synchronization. However the observed benefit with auditory stimuli was only shown in terms of variability of synchronization while for visual stimuli greater improvements were shown with continuous stimuli since both synchronization error and the variability of this error improved compared to a discrete visual stimulus. This may indicate that continuous spatial information is more beneficial for the visual compared to auditory modality. A rationale for these differences between auditory and visual stimuli may lie with the fact that audition is quite strong temporally while vision is quite strong spatially. Thus, by providing more spatial information, as shown by Buekers et al. (2000), this appears to strengthen the perception-action coupling for the visual modality. In contrast, the benefit of providing more spatial information with an auditory stimulus may be limited due to difficulties with perceiving spatial information with this modality, however there is not enough evidence in the literature to confirm this. Little or no research has directly compared spatio-temporal auditory and visual stimuli in a synchronization task. This thesis will aim to fill in this gap by examining the role that spatio-temporal information plays in synchronization with both auditory and visual stimuli.

2.2.4.4 Temporal versus spatio-temporal synchronization

While the two previous sections highlighted studies addressing synchronization with temporal and spatio-temporal stimuli separately an important comparison needs to be made between these two types of stimuli in order to understand the role that spatial information may play in synchronization with visual and auditory stimuli.

Two recent studies focused on improving finger-tapping performance using a variety of different visual stimuli. The first study by Hove & Keller (2010) measured synchronization performance of finger-tapping with a visual flash (temporal stimulus) and alternating images of a finger raised and lowered which resembled a finger tapping motion (spatio-temporal stimulus). One of the aims of the study was to assess whether the addition of spatial information that was congruent with the task could improve synchronization compared to a temporal stimulus (discrete flash). Their results concluded that the addition of spatial information significantly improved synchronization (84% increase in % successful trials with spatio-temporal stimuli) and represented one of the first studies comparing temporal and spatio-temporal visual stimuli with this task. Building on from this research, another study by Hove and colleagues examined more closely these synchronization benefits with spatial information (Hove et al., 2010). Using the same methodology the first part of their study compared 4 different visual stimuli: 1) a visual flash, 2) a horizontally moving bar, 3) a series of images of a bar or 4) finger moving up and down resembling a tapping motion. The two latter stimuli represented an improvement on the previous spatial stimulus that was used in Hove & Keller (2010) moving towards a more continuous stimulus as several images were used between the raising and lowering of the finger or bar. The results showed that while the addition of spatial information significantly improved performance (82% increase in % successful trials) there were no differences between the types of spatial stimuli used. In other words, using a visual stimulus that looks like a “real” finger did not improve the ability to synchronize finger-taps. This result is in line with previous findings that analysed the synchronization of participants arm movements with either a “real” human moving their arm or a robotic arm (Kilner et al. 2003). Overall, the results from the two studies by Hove and colleagues show that the addition of spatial information significantly improved performance in comparison with a temporal visual flash.

Hove et al. (2010) also showed that this improvement was not due to the continuous nature of the stimulus since a fading (non-spatial) stimulus did not improve coordination when compared with the visual flash. More specifically, the results showed that spatial congruency between the movement and the stimulus was a key factor in improving the synchronization performance. Despite these improvements with the spatial stimuli the dominance of discrete auditory stimuli was still found when these two stimuli were compared. The importance of these studies cannot be understated since they represent one of the first attempts to compare a variety of stimuli with different continuity and spatio-temporal information.

The research that has been presented so far has shown the role of spatio-temporal aspects of information for visual and auditory stimuli on movement synchronization. This evidence supports the findings from the perception research that indicates higher temporal acuity for auditory stimuli and higher spatial acuity for visual stimuli. Importantly, this research showed that the nature of visual and auditory stimuli (i.e. with temporal or spatio-temporal information) can significantly impact on coordination dynamics. This discussion places a specific focus 1) on the role that information can play in synchronization and indeed 2) on the importance of information in perception-action coupling. To our knowledge no research has yet directly compared a spatio-temporal visual and auditory stimulus. This thesis will aim to address this gap in the literature by assessing the role of spatial information with continuous auditory and visual stimuli. In contrast to the research presented above a continuous task will be used and it is hypothesised that while the addition of spatial information may improve synchronization for auditory stimuli, vision will ultimately still dominate due to the continuous nature of the task.

2.2.5 A perceptual basis for synchronization

2.2.5.1 The role of relative direction

In an attempt to understand the type of information that is used for stabilizing coordination Bingham and colleagues conducted a series of research studies exploring the importance of perceiving relative phase in stabilising motor coordination. The first of the three studies assessed judgments of relative phase variability using recordings of actual human movement presented on screen as two horizontally oscillating balls (Bingham, Schmidt, & Zaal, 1999). When there was no phase variability in the display (i.e. the stimuli moved at the set phase offset and did not deviate from this), participants' judgments were most reliable with 0° and 180° and they viewed these phases as least variable. It was also indicated that 0° was judged as less variable and more reliably compared to 180°. Overall, the authors indicated that there was an interaction between mean relative phase and phase variability in judging relative phase stability. Their results replicated findings from coordination studies where synchronization is more stable at 0° of relative phase compared to 180° of relative phase, fitting in nicely with the predications from the HKB model. The implication here is that their results may cross over to coordination studies. This perceptual ability, namely perceiving relative phase, may be an important factor in synchronization (Bingham et al., 1999). Since this study used human movement data to present the stimuli, both the specific relative phase and variability of the stimuli could not be fully controlled. Thus, in a follow up study, they used a similar paradigm with computer generated movement data (Zaal et al. 2000). They asked participants to judge both relative phase and phase variability. Their results supported the findings from Bingham et al. (1999) indicating that 1) the judgments of both relative phase and phase variability were more stable at 0° compared to 180° and 2) that phases outside of these two were even more variable.

The final of the three studies (Bingham et al. 2001) used the same paradigm but specifically assessed judgments of relative phase and phase variability with two different frequencies (0.75 Hz and 1.25 Hz). As expected their results supported the two previous studies and also found that as frequency increased stimuli were judged as more variable but only for stimuli that were not at 0° mean relative phase. This latter result is consistent with findings from coordination studies where phase variability increases with frequency for 180° but not 0°. Overall the results gave strong evidence that the perception of relative phase is an important factor in coordination dynamics. This research led to the development of the Perceptually Driven Dynamical model (Bingham, 2004) which focused on the role of perception in rhythmic movements and more specifically on 1) what and 2) how information is used in motor coordination and judgment tasks. Specifically, this model proposed relative direction of movement along parallel orientations as the important information required for synchronization, which depends on relative speed in order for it to be detected (as relative speed decreases it becomes easier to discriminate relative direction). Subsequent studies have provided evidence that strongly supports relative direction as the information that is used for stabilizing coordination in rhythmic synchronization tasks (Wilson et al. 2005; Wilson and Bingham 2008).

One particular study specifically assessed the role of relative direction in a synchronization task. Hajnal et al. (2009) assessed the synchronization of pendulum swinging movements with a horizontally oscillating circular target that was occluded in different locations and by different amounts. Using this methodology the authors were able to answer specific questions that relate to relative direction and Bingham's model. They assessed whether the location of movement information (relative direction) is important for stabilising coordination and also whether the amount of this information influences the stability of coordination. Their results specifically highlighted that when the endpoints of the oscillating visual stimulus were occluded coordination was significantly more variable compared to other occlusion locations (average of 17% increase in variability when endpoints were occluded compared to other occlusion locations). This result supported Bingham's model because relative direction is more salient at the endpoints of a sinusoidal movement, since relative speed is slower at these endpoints. When participants could not clearly detect relative direction it had a negative effect on motor coordination. Another important finding from this study was that despite the significant increase in variability when the endpoints were blocked, participants were still able to complete the task implying that the information between the endpoints provides essential information that is sufficient for the task to be completed.

It would be interesting to apply this model with different stimuli to further understand if similar characteristics can be found across different modalities. For example, previous research has indicated that synchronization with auditory stimuli appears to be more stable when information about relative direction is available (see Rodger & Craig, 2011 in Section 2.2.3.3.2). However, the extent to which this modality relies on the perception of relative direction is unclear. This thesis will address this question by applying the same paradigm used by Hajnal et al. (2009) with visual and auditory stimuli in a pendulum based synchronization task. It is hypothesised that while the endpoints of an auditory stimulus will still play a key role in stabilising the coordination it may play an even more important part in auditory synchronization due to the poor spatial saliency of the stimulus.

2.2.5.2 Anchoring and task-specific information in stimuli

The use of occlusion is quite a unique method for assessing the importance of perceiving relative phase in coordination dynamics but other paradigms can also be employed to explore this perceptual basis for perception-action coupling. Roerdink, Peper, & Beek (2005) investigated the use of visual feedback on in-phase and anti-phase synchronization of hand tracking movements. Their feedback was similar to the stimuli presented in the judgment task conducted by Bingham and colleagues. The target stimulus, a ball, oscillated horizontally and the participant's movements were displayed in real time as another ball above the target. The perception of relative phase was modified in two conditions where the participant's ball moved in the same (correct feedback) or opposite (mirrored feedback) direction as their hand movements. Their results supported the findings from the judgment studies, for the in-phase conditions when feedback was congruent with the hand movements synchronization error was significantly reduced compared to when it was incongruent (24% improvement with congruent feedback). When the feedback was congruent with the direction of the target's movements it helped to stabilise anti-phase movements compared to when no feedback was present (improvement of 43%). This implies that when additional congruent information about relative direction is provided, it helps to stabilise coordination.

The study also assessed how gaze direction can influence the stability of coordination. By relating gaze direction to reductions in variability, the authors hoped to identify where important task specific information is available and picked up. To assess this variability in the movement, they used a variable know as anchoring. Anchoring is defined as regions of reduced spatial or temporal variability (Beek, 1989). These characteristics are typically found at the endpoint of movement (Roerdink et al. 2008). Researchers have implied that these local reductions in variability correlate to important task-specific information required for motor coordination (Beek 1989). Spatial anchoring is a measure of the participant's variability at the endpoint independent of the stimulus while temporal anchoring is the variability in the asynchrony between the stimulus' arrival time at an endpoint and the corresponding time of the participant's arrival. When gaze direction was fixated on either the left or right endpoint more spatial anchoring was observed at these specific regions, respectively (20% increase in anchoring for left endpoint gaze and 40% increase in anchoring for right endpoint gaze), while when gaze was fixated in the centre of the screen or when it pursued the target spatial anchoring was found to be similar at both the left and right endpoints. Indeed these results seem to indicate that relevant task-specific information seems to be available at the endpoints of the stimulus. The findings also provide further support for the role of perceiving relative direction in synchronization for two reasons. Firstly, the very presence of these anchoring points at the discrete endpoints of the movement corresponds with the fact that relative direction is most salient at these locations. Secondly, when the saliency of relative direction at one endpoint was reduced, for example when gaze was fixated on the opposite endpoint, this caused an increase in the variability of movement at the less salient endpoint which supports the findings from Hajnal et al. (2009) who also found increased variability when endpoints were not visible.

Further research by Roerdink and colleagues using this same paradigm established that while gaze direction clearly reduced spatial anchoring, it did not reduce the temporal anchoring (Roerdink et al., 2008). This indicates that the influence of gaze direction is limited to the spatial control of movement and does not impact on the temporal organization. These findings also highlight the importance of examining both spatial and temporal aspects of synchronization in order to establish a full picture of the dynamics of the system.

The research discussed in the last two sections clearly shows the significant influence of informational constraints on the ability to synchronize with an external rhythmic stimulus. These informational constraints related to how stimuli were presented namely with temporal or spatio-temporal information. Within the tapping literature the use of temporal stimuli is quite popular and the auditory modality appears to dominate over vision in terms of synchronization performance. In contrast with this when spatio-temporal information is provided vision seems to dominate over audition. Each modality appears to have their own strengths in either the spatial or temporal domain. The research presented shows how changes in the type of information provided can affect synchronization and some researchers have even begun to investigate this perceptual basis for motor coordination. Bingham (2004) formalised this idea in his Perceptually Driven Dynamical model. Research has since provided support for some of the predictions made by the model, namely that the perception of relative direction is a central part of perception-action coupling. The research presented was mainly concerned with identifying the role of auditory and visual information in a synchronization task. While assessing each of these sensory modalities on their own is important, a better understanding of multisensory integration of visual and auditory information would provide a more realistic view of how motor coordination may occur in daily life. The next section will specifically deal with synchronization with multisensory stimuli and how the congruency between these modalities can influence their integration.

2.2.6 Synchronization with multisensory stimuli

The focus of the discussion so far has been mostly related to synchronization with unimodal stimuli and while much has been established about the synchronization of movements to these stimuli, it is not a true reflection of how we experience our environments. In real life, the perception of a given stimulus often occurs through multiple modalities (Haywood and Getchell 2005) and virtually all action gives rise to multisensory stimulation (Stoffregen & Bardy, 2001). The combining of this information from multiple senses allows for a more robust and unified percept of a given event (Burr and Alais 2006). Much of what is known about multisensory integration can be derived from research on perception, which involves manipulating the temporal and spatial congruency of the modalities. The congruency between modalities can greatly influence the overall effect that multisensory stimuli can have on perception. This was demonstrated in Section 2.1 of this thesis by the phenomenon known as the *ventriloquism effect*. When two stimuli are presented together in terms of timing but are spatially incongruent, perception of an auditory stimulus can be "captured" by a visual stimulus, even when the latter is to be ignored, resulting in judgments that are closer to the visual rather than the auditory stimulus. This phenomenon is called *spatial ventriloquism*. On the other hand when the same stimuli are in the same location but lack temporal congruency the judgments of the visual stimulus can be "captured" by the auditory stimulus, *temporal ventriloquism*. The ability of a visual and auditory stimulus to influence each other closely relates to the strength of these modalities in the spatial and temporal domains, respectively. Importantly, these effects are not limited to perception, as similar evidence exists in synchronization studies where the spatial and temporal congruency between two modalities is manipulated.

Repp & Penel (2002) found evidence suggesting that the integration of sensory information can occur even when a distractor stimulus is supposed to be ignored. In their study participants had to synchronize finger tapping with a target stimulus while a distractor stimulus, from a different modality, was also present. Their results indicated that the auditory distractor affected the timing of taps significantly more than the visual distractor (conflicting auditory distractor represented 84.3% of the overall influence on responses to event onset shifts with the same modality). While this does not confirm the presence of temporal ventriloquism it does strongly support the high temporal saliency of auditory information. When presented in a bimodal condition this information is integrated even when it is supposed to be ignored. These results were in support of previous work using the finger-tapping paradigm assessing the effect of auditory and visual distractors (Repp & Penel, 2004). Hove et al. (2013) were able to show that a visual stimulus presented as a bouncing ball was as effective at distracting finger tapping as an auditory stimulus (auditory metronome). This shows that while previously visual stimuli without spatial information were not as effective as auditory stimuli in terms of affecting tapping performance (Repp & Penel, 2002, 2004) the addition of this spatial information appears to improve the role of a visual stimulus as a distractor (Hove et al., 2013). This research highlights the important effects that congruency between a stimulus and a movement can have on synchronization with multisensory stimuli. These results also highlight how the strength of each sensory modality in their respective domains (spatial and temporal) can also impact on synchronization.

Other studies, analysing synchronization, have placed a strong emphasis on multisensory integration by manipulating the congruency between these two modalities. In these studies participants are required to synchronize with both modalities presented either congruently (simultaneously) or incongruently (e.g. in anti-phase to each other). Within these studies the finger-tapping paradigm was usually used in combination with a focus on tactile and haptic stimuli, which are closely related to this task. One such study by Lagarde & Kelso (2006) used this methodology to assess synchronization with haptic and auditory stimuli presented in 1) unimodal, 2) multimodal simultaneous or 3) multimodal anti-phase conditions. For the multimodal anti-phase conditions flexion of the finger corresponded to the auditory stimulus while extension corresponded to the haptic stimulus and vice versa. Globally, these results indicated that variability of relative phase was higher for the multimodal anti-phase (approx. 24° SD relative phase) compared to multimodal simultaneous (approx. 17° SD relative phase) conditions (represents a 40% increase n variability with multimodal anti-phase conditions). Similarly, there were twice as many transitions from the required pattern, indicating more instability, as frequency of oscillation increased for the multimodal anti-phase conditions compared to the multimodal simultaneous conditions. This is an important finding as it implies that congruency between the presentation of modalities is an important factor for stabilising multisensory synchronization. Similar results have also been found in complex bimanual tapping tasks that require a 3:2 polyrhythmic movement of left and right index fingers (Lagarde, Zelic, & Mottet, 2012). In this study the presentation of auditory and haptic information in anti-phase to each other destabilised the coordination resulting in more variability and larger asynchronies.

An earlier study by Kelso et al. (2001) used a slightly different haptic stimulus to demonstrate a clear benefit of multimodal information. In their study the finger-tapping paradigm was employed with different combinations of auditory and haptic information. While the auditory stimulus was a discrete beep, the haptic information was derived from contract of the synchronizing index finger with a physical stop. Participants were only ever attempting to synchronize either flexion or extension of the index finger with the auditory stimulus while sometimes the haptic contact was present either in-phase with the beep or anti-phase to it. The results supported previous work (Lagarde and Kelso 2006; Lagarde et al. 2012) showing that when the modalities were presented in anti-phase to each other coordination was destabilised (average of 60% of trials displayed transitions to a different behaviour). However, in contrast to this previous work Kelso et al., (2001) found that coordination was actually stabilised when the haptic information was coincident with the auditory stimulus (average of 1.5% of trials displayed transitions), even more so than in their unimodal auditory condition (average of 27.5% of trials displayed transitions). The authors attributed this benefit to a possible reduction in the attentional demands for this condition. Indeed, their results indicated that congruent auditory and haptic information is integrated to significantly improve synchronization.

This finding was supported by recent research that used haptic information that was an additional synchronization point instead of a contact point. Wing, Doumas, & Welchman (2010) assessed finger tapping of the right index finger to an auditory discrete beep and a continuous haptic stimulus presented in unimodal and bimodal conditions. The haptic stimulus constituted passive movements of the left index finger, controlled by a robot, representing a flexion-extension movement. When these stimuli were presented simultaneously variability of timing was significantly reduced (average of 23 ms asynchrony SD) compared to both unimodal conditions (average of 31 ms for haptic and 41 ms for auditory asynchrony SD), again providing strong evidence for multisensory integration (representing a 34% increase with haptic and a 78% increase with auditory in terms of variability). In this case the haptic stimulus was unique since it was a continuous movement rather than a discrete vibration, indicating that information from different modalities can be integrated even when their continuity differs.

Zelic, Mottet, & Lagarde (2012) investigated the effect of providing auditory and haptic stimuli with different congruencies in a juggling task. Their results seemed to contradict the findings discussed above. When haptic information was provided simultaneously in the unimodal conditions it significantly increased the variability of the juggling. However, in the bimodal conditions when the multisensory information was presented in anti-phase to each other spatio-temporal variability was significantly reduced. Based on these findings the authors suggested that the multimodal anti-phase condition was able to override the detrimental effect of haptic stimuli not by acting locally on each hand but by globally improving the overall coordination pattern since the anti-phase condition specified the relative timing between the two hands. The specific spatio-temporal nature and complexity of the juggling task and the fact that the participants were not specifically asked to synchronize with the stimuli may contribute to the differences observed with this study and those previously discussed. Thus, this bimodal benefit observed when the stimuli were in anti-phase to each other may be limited to this specific task. This is important to highlight as it is known that when two stimuli are presented simultaneously, in other words, when they have spatial and temporal congruency (perceived as information from the same event), performance is improved to a level that is greater than that predicted by summing their individual influences (Carson and Kelso 2004). This is known as *response amplification* and the results presented above appear to be in contrast to this well-established phenomenon in multisensory integration. Overall, multisensory integration was observed in several studies but so far the studies mentioned above did not address the level of multisensory integration, in other words, was this sensory information optimally integrated?

2.2.6.1 Optimal integration and multisensory synchronization

The main aim of Wing and colleagues' (2010) experiment was to test predictions of the Maximum Likelihood Estimation (MLE) model. As discussed in Section 2.1.3.1 this model is a weighted linear sum of the reliability of each sensory modality and assumes that multisensory stimuli are integrated based on their reliability where more weight is given to the modality that is more reliable. Importantly the model also predicts that when modalities are presented together the variability will be lower than the individual counterparts. Wing and Colleagues tested this model by reducing the reliability of the auditory stimulus by adding jitter to this stimulus in both the unimodal and bimodal conditions. The non-jitter conditions, discussed above, supported the MLE model since the combined variability was lower than both unimodal conditions. However, as the amount of jitter in the auditory condition increased, the resulting behaviour moved closer to the auditory stimulus and not towards the more reliable haptic stimulus (since the haptic stimulus never contained any jitter). This is in contrast with the MLE model since it predicts that as reliability is reduced in one modality a higher weighting is given to a stimulus that is more reliable. These results suggest a dominance of the auditory modality even though it is less reliable than the tactile stimulus and highlights the limitations with the MLE model.

Elliott et al. (2010) used the same levels of jitter and the same task as Wing and colleagues but compared unimodal and bimodal conditions of visual, auditory and haptic stimuli. Using an extended version of the linear phase correction model they were able to predict the reduced synchronization variance with bimodal compared to unimodal conditions, based on the assumptions from the MLE model that multisensory cues are optimally integrated. This allowed the authors to isolate the noise associated with each sensory modality individually and then to use these estimates to test predictions of the optimal weighting of the modalities in the bimodal conditions. Their results indicated a dominance of auditory stimuli in bimodal conditions when jitter was high for this modality (asynchrony increased by 57% from the no jitter to high jitter bimodal conditions). These results support previous perception studies that also found sub-optimal weighting of modalities in favour of auditory stimuli in temporal based tasks (Shams et al. 2000; Burr et al. 2009; Gori et al. 2012). Importantly, the authors proposed that this observed dominance could be due to the information from the two modalities being perceived as separate events. Thus, these modalities may have fallen outside the temporal window of integration (see Section 2.1.3) and due to the strong reliability of auditory stimuli for timing the participants synchronised with this modality. This explanation could also apply to the results from Wing and colleagues given that the methodologies were very similar. Importantly, it indicates the requirement of congruency in order for multisensory stimuli to be successfully integrated. Despite these deviations from the model their results supported the bimodal benefit observed in Wing and colleagues study and expanded this bimodal benefit to include combinations of tactile-visual and tactile-auditory stimuli.

Further support for this bimodal benefit can be found with continuous tasks as well. Varlet et al., (2012) assessed the ability to synchronize wrist pendulum swings with auditory and visual stimuli that were presented in both unimodal and bimodal conditions. The stimuli did not contain any spatial information but importantly the continuity was manipulated and thus the stimuli were presented in discrete or continuous modes. Overall the results indicated that when the stimuli were presented together in the bimodal conditions the sensory information could be integrated to enhance coordination compared to the unimodal conditions. When the individual bimodal conditions were compared there was evidence that coordination was better when the continuity of the modalities differed compared to when they had the same continuity. This may be related to the fact that participants led continuous and followed discrete stimuli thus when these two different modes of continuity were combined in the bimodal condition the individual tendencies of leading and following the stimulus were combined creating coordination that was closer to zero, i.e. midpoint between the leading and following values. The authors suggested that the addition of spatial information in future research might increase the weight of the visual modality in the coordination, as vision particularly salient in this domain. This relates to one of the key objectives of this thesis: investigating the role of spatial information in a synchronization task.

2.2.7 Overall conclusion

The nature of multisensory integration appears to be mediated by the temporal and spatial congruency between auditory and visual stimuli. In general the studies discussed above appear to indicate that when sensory information is presented in anti-phase to each other (incongruency in modalities) coordination is destabilised. When these stimuli are presented with spatial and temporal congruency the resulting performance is improved to a level greater than that of the summed individual influence. Hence, numerous studies have indicated that sensory information can be integrated from different modalities in order to enhance synchronization in comparison with unimodal stimuli. The purpose of this thesis will be to examine the influence of temporal and spatio-temporal information on synchronization with auditory and visual stimuli presented in unimodal and bimodal conditions. The aim is to dissociate these two elements in order to establish the specific role that spatial information may play in stabilizing coordination while at the same time addressing questions relating to synchronization with auditory and/or visual stimuli that only contain temporal information.

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Chapter 3: The Supplementation of Spatial Information Improves Coordination

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3.2 Introduction

The pioneering work by Gibson (1986) on the perception of visual information reflects the key role of visual information in coordinated action. To date, extended research has focused on understanding how humans visually coordinate their actions using stimuli in the form of an oscillating object (Roerdink et al. 2005; Wilson et al. 2005; Schmidt et al. 2007; Roerdink et al. 2008; Hajnal et al. 2009). While these studies have identified important aspects of visual coordination and fundamental dynamics of coordination in terms of variability and stability, further research is required to assess the specific role of spatio-temporal information in coordination. Spatio-temporal information can play an important role in many motor skills, such as catching a ball. In order to catch the ball, accurate perception of both spatial and temporal information is required: moving your hand to the correct location and at the right time, respectively (Oudejans et al. 1996). The importance of spatio-temporal information is evidenced in the previous example and this article aims to analyse the role of spatio-temporal information in a coordinated task by supplementing an oscillating temporal stimulus with spatial information.

Much has been revealed about how we coordinate with visual stimuli in the spatio-temporal domain over the last two decades (Zaal et al. 2000; Bingham et al. 2001; Bingham 2004; Kilner et al. 2007; Stanley et al. 2007; Lopresti-Goodman et al. 2008). For example, Bingham's work on the perceptually driven dynamical model for coordination (Bingham 2004) has led to research exploring what information is used for coordination with an oscillating visual stimulus. One such article by Hajnal et al. (2009) highlighted how coordination can be negatively affected when information about the relative direction of movement is reduced by occluding the end points of an oscillating square. In other words, when the stimulus was supplemented with more information, i.e. the stimulus was not occluded, coordination improved. This concept of supplementing a stimulus with additional information is what the current article is investigating by supplementing a temporal stimulus with spatial information. While a spatio-temporal stimulus is commonly found in the literature as discussed above there is a lack of research utilising a visual stimulus exclusively represented in the temporal domain.

Few studies have assessed coordination with a continuous visual stimulus exclusively in the temporal domain. For example, Varlet et al. (2012) examined how the nature of a visual stimulus, whether it is discrete or continuous, significantly effects coordination. The results from Varlet et al. (2012) supported previous findings (Buekers et al. 2000; Hove et al. 2010), revealing that coordination was superior and more stable with the continuous stimulus (fading square) compared to the discrete stimulus (flashing square). Based on these results, there appears to be a preference of the motor coordination system for continuous visual information perhaps due to a weakening of the perception-action coupling when discrete stimuli are present as less information is available. This continuous stimulus (fading square) exclusively contained temporal information. A similar stimulus will be used in this article.

The current article will essentially be building on the findings from Varlet et al. (2012) by taking a deeper look at their temporal stimulus and assessing how the supplementation of spatial information to this temporal stimulus can affect coordination. This will be assessed by asking participants to synchronize movements of a handheld pendulum with two different visual stimuli, one containing only temporal information and the other containing both spatial and temporal information. Evidence from the perception literature indicates that visual perception is particularly strong within the spatial domain (Howard and Templeton 1966). This has been supported by research from the field of perception-action that has shown improvements in synchronization performance with visual stimuli when spatio-temporal information compared to only temporal information is available (Buekers et al. 2000; Hove et al. 2010). Based on this evidence it is hypothesised that synchronization performance in the current study will be significantly better with the spatio-temporal compared to the temporal stimulus.

3.3 Methodology

3.3.1 Participants

Twelve volunteers (8 females and 4 males) between the ages of 18 and 24 years (22.4 yrs. ±2.9) took part in the experiment. All participants were right handed, had normal or corrected to normal vision and no known history of a neuromuscular deficit that would affect their participation. Colour blindness was assessed using a series of five Ishihara pictures. Any participant with any form of colour blindness was removed from the experiment. No compensation was given to the participants for their involvement in the experiment. The procedure for the research received full ethical approval from the Dublin City University Research Ethics Committee (DCUREC/2011/038).

3.3.2 Experimental setup

Participants sat in a height adjustable chair with a forearm support and gripped an aluminium pendulum with their right hand. Fixed to a 14 cm long handle, the pendulum had a length of 49 cm and a weight of 53 g attached at the end. Its eigenfrequency was 0.90 Hz. Participants were prevented from viewing the pendulum's movements with a wooden cover and the arm of the participant was also concealed using a sliding panel. Participants swung the pendulum in a darkened room, through the frontal plane by pronating and supinating their forearm while wearing noise cancelling headphones. The screen displayed the stimuli and was placed at eye level approximately 1 m from the participants. Data from the pendulum was recorded at 200 Hz using a National Instruments DAQ device (National Instruments, USB-6229) and stored for further analysis.

3.3.3 Stimuli

The stimuli consisted of two different oscillating visual signals presented on a screen with a white background. The spatio-temporal stimulus appeared as a green square (30 × 30 mm) oscillating horizontally across the screen in a sinusoidal fashion with an amplitude of 40 cm. The temporal stimulus was similar to the "Visual Continuous" stimulus used by Varlet et al. (2012) and appeared as a stationary square (30 × 30 mm) in the centre of the screen that continuously faded in colour between a black and green colour in a sinusoidal fashion. The various stages of these stimuli are presented in Figure 1. Both of these stimuli were created using Labview software (National instruments, Labview 10.0).

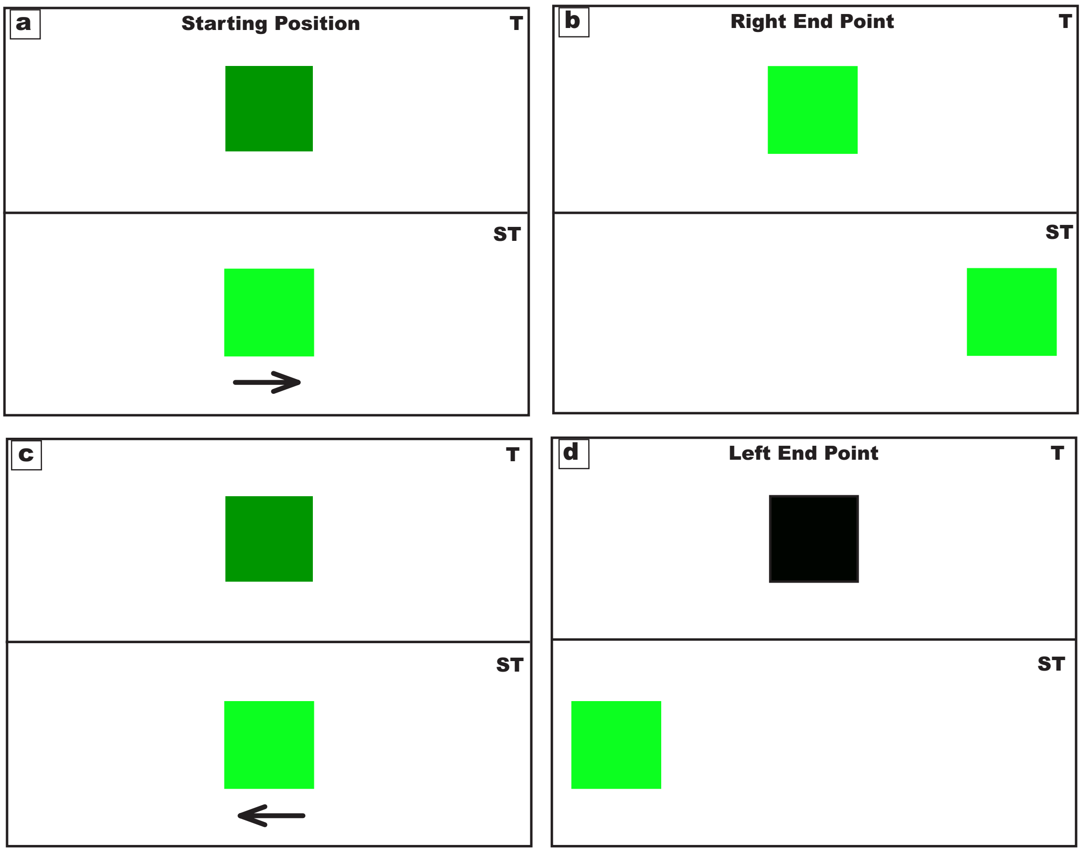

Figure 1 Stages of the two Stimuli

The top half of Figure 1a-d displays the stages of the temporal stimulus (T) while the bottom half displays the spatio-temporal stimulus (ST). Figure 1a shows the starting point of each stimulus, Figure 1b the first end point of the stimuli, Figure 1c the return to the starting/mid point and Figure 1d the second end point of the stimuli.

3.3.4 Procedure

Upon arrival participants were handed an information sheet about the experiment and were asked to sign an informed consent form. Following this, the experiment was explained in three parts, 1) preferred frequency calculation, 2) familiarisation and 3) experimentation. The subjects were told to move the pendulum with an amplitude of 45 degrees to the right and 45 degrees to the left from the resting position of the pendulum. An example of the experimental setup is shown in Figure 2. For the preferred frequency calculation participants were asked to swing the pendulum for two minutes at a pace that was ‘most comfortable’ for them with their eyes shut. The preferred frequency of each participant was used to create two additional frequencies: +20% of preferred and -20% of preferred. After a pre-test using a ±15% frequency range the authors increased the range to ±20% to allow for a clearer difference in frequencies without creating a coordination task that was too difficult for the participants.

During the familiarisation stage the temporal and spatio-temporal conditions were played once for the participants and additional plays were provided if requested by the participant or required by the experimenter in order to ensure an understanding of the different experimental conditions. For the temporal stimulus, participants had to reach the left end point when the black was most salient (Figure 1d) and the right end point when the green was most salient (Figure 1b). Likewise, for the spatio-temporal stimulus, participants had to swing to the left as the square moved left (Figure 1d) and to the right as the square moved right (Figure 1b), synchronizing the end point of the movements with the square’s end points. The familiarisation was conducted at a frequency of 10% slower than their preferred frequency.

The experiment consisted of three frequencies (+20%, preferred and -20%) and the two visual conditions (spatio-temporal and temporal). Participants completed three randomised blocks of six conditions. There was a 30 second break after each 40 second trial and a five minute break between blocks.

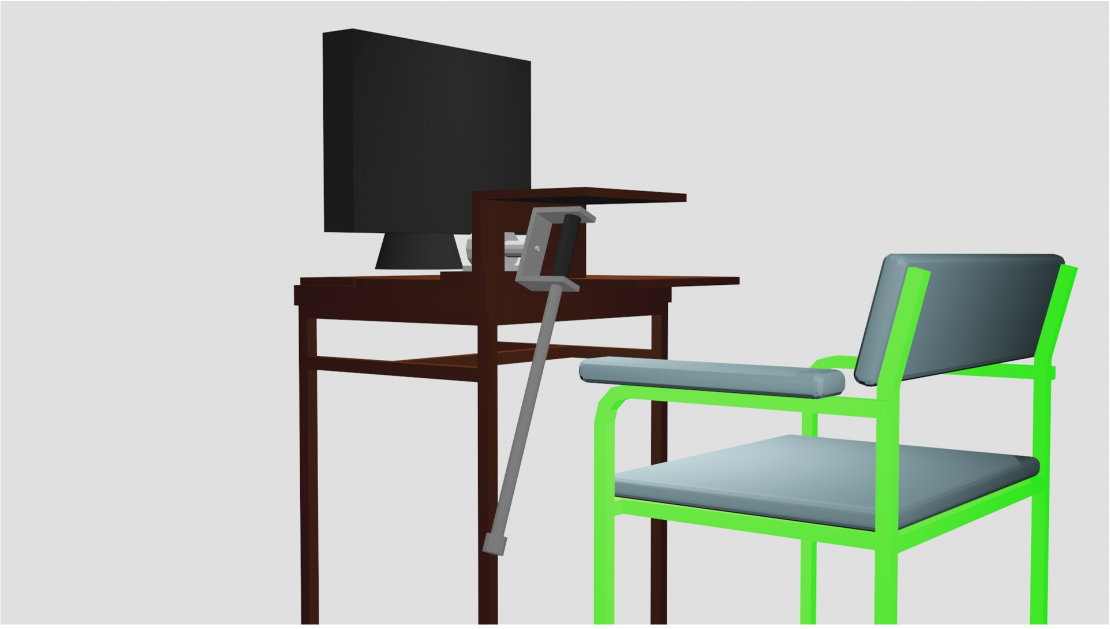

Figure 2 Example of experimental setup

3.3.5 Data reduction

The first 10 seconds of data were removed and the remaining 30 seconds were low pass filtered using a 18 Hz Butterworth Filter. Data were then normalised between +1 and -1 using min max scaling. All data were averaged across each of the three trials for the six experimental conditions. Cross-spectral Coherence (CSC) was used to assess the degree of coordination between the two time series in the frequency domain. CSC evaluates the correlation between two times series at a given frequency and produces an index from 0 (no coherence) to 1 (complete coherence). Given the fact that human movement is variable, specifically in terms of frequency (Varlet and Richardson 2011), CSC provides a useful way of assessing a participant’s deviation from the intended frequency. In order to assess the degree of coordination between the participants and the stimulus, continuous relative phase (CRP) was assessed. CRP was calculated using a Hilbert Transform and scaled between 0° and 180°. The standard deviation (SD) of CRP was also calculated to assess the variability of the coordination throughout the full movement.

To assess whether participants preceded or followed the stimulus mean asynchrony was calculated. Mean asynchrony takes the time of the participant at the min and max points of the oscillation and subtracts this from the time of the stimulus at the equivalent points. The min and max points equate to the right and left end points of the movements respectively. A positive value indicates that the participant followed the signal by arriving late and a negative value means that they preceded the signal by arriving earlier than the stimulus at the end point. An assessment of early and late arrivals at the end points provides insight into how the perception-action dynamic changes across the range of frequencies and the type of stimuli. In order to assess the deviation from the intended movement at the end points, spatial anchoring was calculated. Spatial Anchoring is the standard deviation of the participant's movement at the end points. A low value for anchoring indicates a reduction in the variability of the movement at these end points. The anchoring data were divided into two categories, right and left end point of the movement allowing for an analysis of coordination specifically at the most salient points of the stimuli, i.e. the end points.

3.3.6 Statistical analysis

All the statistical analysis was performed using SPSS (IBM SPSS Statistics 19) using the averaged data across the three trials and the 12 participants. To assess the conditions and compare them against each other a repeated measures analysis of variance (ANOVA) was conducted for all of the variables. Sphericity was assessed for each of the variables and the Greenhouse and Geisser's correction for the degrees of freedom was applied when sphericity was not met. Post Hoc analysis using Bonferroni's confidence interval was carried out on the frequencies for CSC, CRP, mean asynchrony and anchoring. The size of the effect for all of the ANOVA analysis was reported by means of the partial eta squared (η^2_p).

3.4 Results

3.4.1 Cross-spectral coherence

A 2 (Stimulus) × 3 (Frequency) repeated measures ANOVA was conducted on the mean coherence values for each participant. The results revealed a significant main effect of Stimulus, $F(1, 11) = 12.3$, $p < .05$, $\eta^2_p = .53$. As shown in Figure 3 the temporal stimulus produced significantly less coherence than the spatio-temporal stimulus. There was also a significant main effect found for Frequency, $F(2, 22) = 4.43$, $p < .05$, $\eta^2_p = .29$. The post hoc comparisons revealed that the +20% conditions had a significantly higher coherence value compared to the -20% conditions. There was no significant interaction between Stimulus and Frequency, $F(1.25, 13.78) = 0.08$, $p > .05$, $\eta^2_p = .01$.

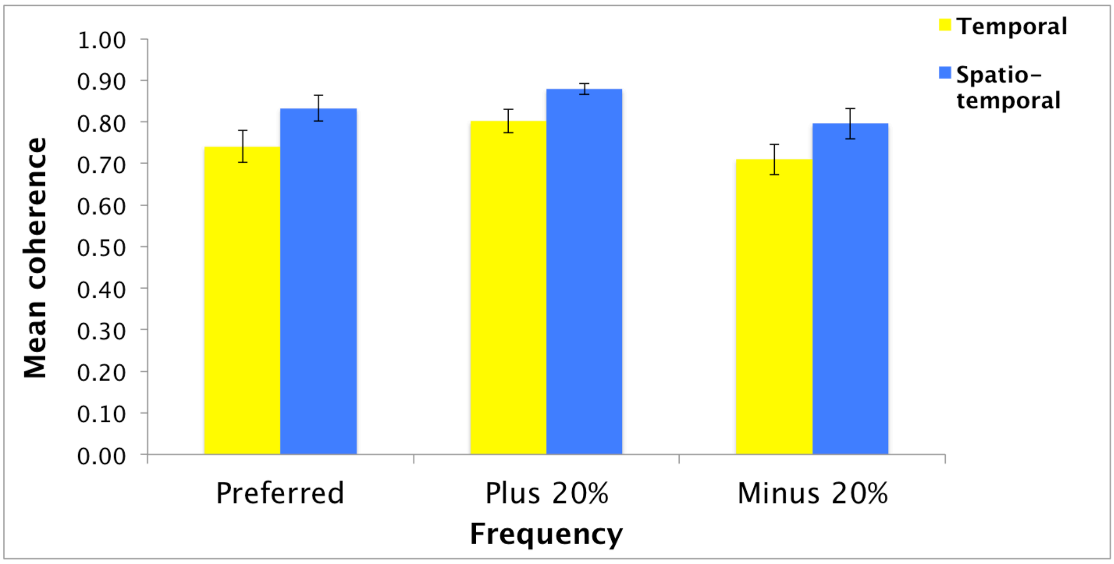

Figure 3 Mean Cross-spectral Coherence

3.4.2 Continuous Relative Phase

The mean CRP angles were inputted into a 2 (Stimulus) × 3 (Frequency) repeated measures ANOVA. The analysis resulted in a significant main effect of Stimulus, $F(1, 11) = 10.13$, $p < .05$, $\eta^2_p = .47$. Lower CRP angles were found for the spatio-temporal stimulus compared to the temporal stimulus. There was a significant main effect of frequency, F(1.23, 13.53) = 5.94, $p < .05$, $\eta^2_p = .33$ with the post hoc analysis revealing that the +20% conditions had lower CRP angles than -20%. Figure 4 displays the mean CRP angles for each of the six conditions. The interaction between stimulus and frequency was not found to be significant, F(2, 22) = 0.12, $p > .05$, $\eta^2_p = .01$.

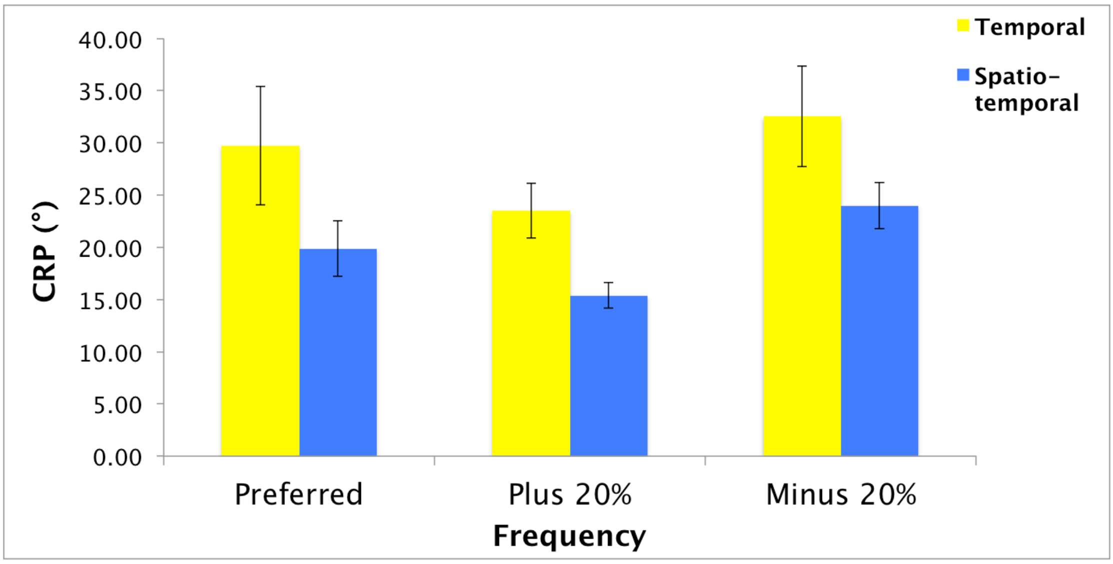

Figure 4 Mean Continuous Relative Phase

A 2 (Stimulus) × 3 (Frequency) repeated measures ANOVA was run on the standard deviation of CRP and revealed a significant main effect of stimulus, F(1, 11) = 17.26, $p < .05$, $\eta^2_p = .61$. The standard deviation of CRP results ranged from 11.63° to 24.7°, indicating low to high variability respectively. The temporal stimulus (SD = 22.04°) produced higher levels of standard deviation than the spatio-temporal stimulus (SD = 13.24°) for all frequencies. There were no significant findings for frequency, F(2, 22) = 1.75, $p > .05$, $\eta^2_p = .14$. There was no significant interaction found between stimulus and frequency, F(1.35, 14.87) = 0.3, $p > .05$, $\eta^2_p = .03$. Figure 5 displays the mean SD CRP angles for each of the six conditions.

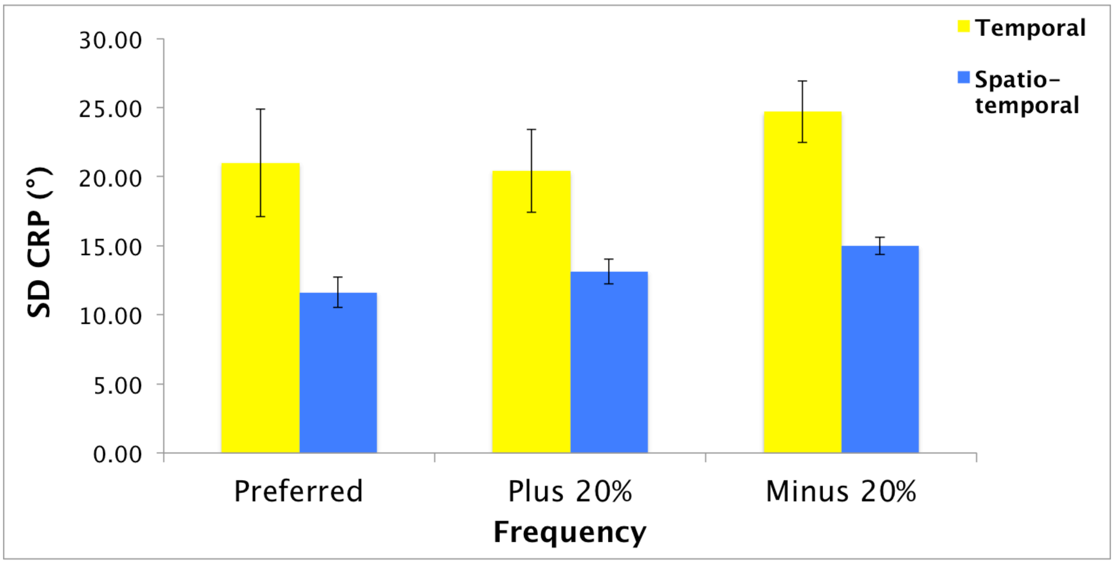

Figure 5 Mean Standard Deviation of CRP

3.4.3 Mean Asynchrony

Mean asynchrony was analysed through a 2 (Stimulus) × 3 (Frequency) repeated measures ANOVA. Participants predominantly preceded the stimulus with the temporal preferred (-168 ms), spatio-temporal -20% (-128 ms) and temporal -20% (-114 ms) conditions arriving the earliest before the stimulus. The spatio-temporal preferred condition preceded the stimulus by -56 ms while the temporal +20% condition only preceded the stimulus by -5 ms. Spatio-temporal +20% (60 ms) was the only condition where participants followed the stimulus. There were no significant differences found for stimulus, $F(1, 11) = 0.79$, $p > .05$, $\eta^2_p = .07$ or frequency, $F(2, 22) = 1.92$, $p > .05$, $\eta^2_p = .15$. Also no significant interaction was found between stimulus and frequency, $F(2, 22) = 0.58$, $p > .05$, $\eta^2_p = .05$. A comparison of the right and left end point was carried out using a 2 (Stimulus) × 3 (Frequency) × 2 (End Point) repeated measures ANOVA. It produced no significant effect for stimulus, $F(1, 11) = 0.79$, $p > .05$, $\eta^2_p = .07$, frequency, $F(2, 22) = 1.92$, $p > .05$, $\eta^2_p = .15$ or end point, $F(2, 22) = 0.00$, $p > .05$, $\eta^2_p = .00$. Figure 6 displays the mean asynchrony values for each of the six conditions.

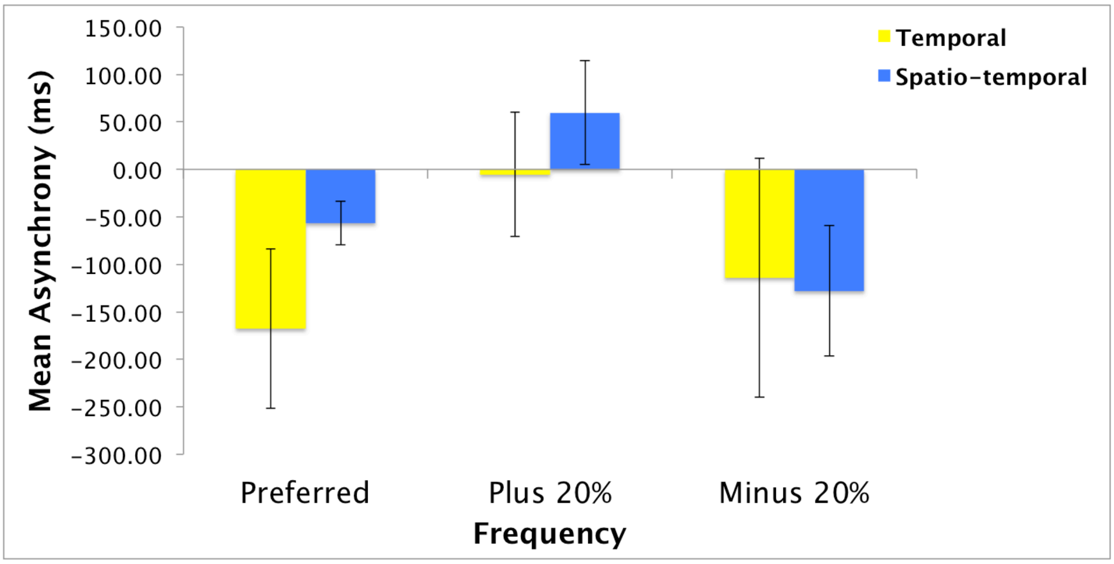

Figure 6 Mean Asynchrony

3.4.4 Spatial Anchoring

The spatial anchoring was analysed using a 2 (Stimulus) × 3 (Frequency) × 2 (End Point) repeated measures ANOVA. The results indicated a significant main effect for stimulus, F(1, 11) = 5.25, $p < .05$, $\eta^2_p = .32$, with the spatio-temporal stimulus (mean left = 0.221 and mean right = 0.227) producing significantly more anchoring than the temporal stimulus (mean left = 0.242 and mean right = 0.249). Frequency was also found to be significant, F(2, 22) = 13.14, $p < .05$, $\eta^2_p = .54$. The post hoc analysis revealed that the +20% conditions (mean left = 0.211 and mean right = 0.216) produced significantly more spatial anchoring compared to the -20% conditions (mean left = 0.254 and mean right = 0.266). There were no significant differences between the right and left end points, F(1, 11) = 1.58, $p > .05$, $\eta^2_p = .13$. None of the interactions were significant: End Point × Stimulus F(1, 11) = 0.19, $p > .05$, $\eta^2_p = .12$, End Point × Frequency F(2,22) = 013, $p > .05$, $\eta^2_p = .01$, Stimulus × Frequency F(2,22) = .73, $p > .05$, $\eta^2_p = .06$, End Point × Stimulus × Frequency F(2,22) = .79, $p > .05$, $\eta^2_p = .07$. Figure 7 displays the overall (mean of left and right) spatial anchoring values.

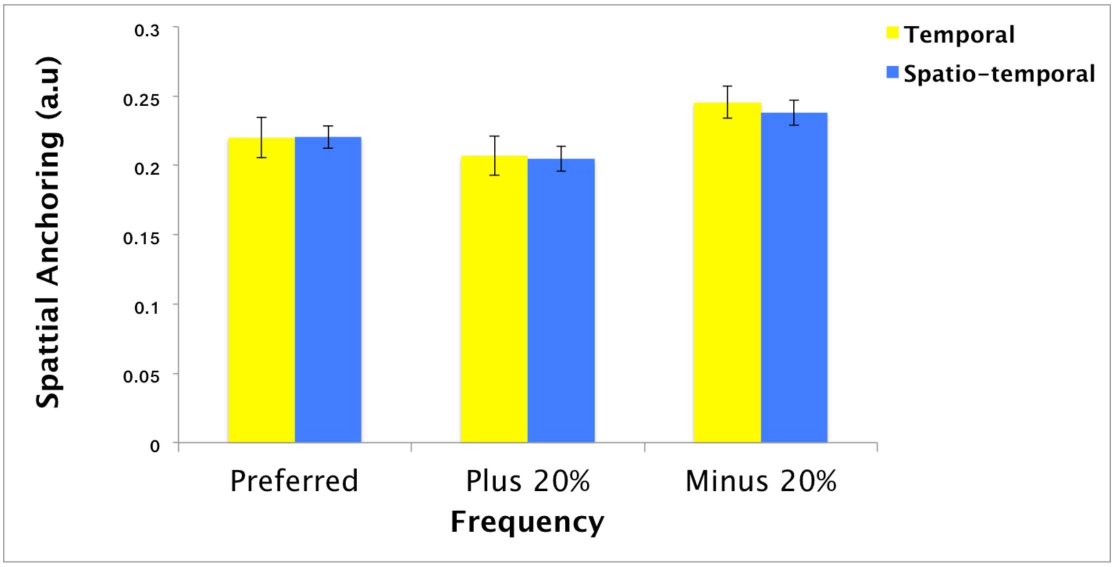

Figure 7 Overall Spatial Anchoring

3.5 Discussion

The current experiment examined the effect of supplementing a temporal visual stimulus with spatial information on coordination. The temporal condition maintained good levels of coordination, as evidenced by the relatively low CRP values shown in Figure 4, displaying a resilience of the motor system to adapt to changes in the environment when less information is available. Ultimately the presence of spatio-temporal information produced more stable coordination, as evidenced by the CRP and SD CRP results, in line with the hypothesis. These results highlight the importance of perceiving both the spatial and temporal information of a visual stimulus. Additionally some questions are raised regarding synchronizing with a temporal stimulus as it has not been extensively used in the literature and further investigation is required using this type of stimulus.

We know from previous research that detecting the relative direction of movement is essential for coordination with a oscillating visual stimulus (Bingham 2004; Wilson et al. 2005; Wilson and Bingham 2008; Hajnal et al. 2009). Hajnal et al. (2009) found that reducing the amount of information available about relative direction by blocking parts of the end points of a horizontally oscillating square, negatively affected coordination. In the current article, the information available was reduced: there was no spatial information in the temporal stimulus, and which consequently diminished the detection of relative direction. The lack of spatial information in the stimulus had a damaging effect on the coordination producing higher values of CRP. This presents an interesting question about how coordination is achieved when spatial information of a stimulus is removed. With our temporal stimulus one could argue that the most important components may be the end points. This could imply that participants may have difficulty perceiving the colour that is available between the dark black and bright green end point colours, or that this information is not as advantageous for coordination and is only passively perceived or ignored. Further research is needed to investigate how people perceive this type of stimulus and which component(s) help ‘anchor’ the coordination.

The saliency of the temporal stimulus allows for an interesting discussion about how participants perceive this type of stimulus and raises questions about whether or not the stimuli are indeed equally salient. When dealing with temporal stimuli saliency can sometimes be an issue as discussed in Varlet et al. (2012). They suggested that using less salient stimuli in their experiment might have resulted in greater observed differences between their discrete and continuous visual stimuli. Regarding the current findings, we can assume that the spatio-temporal stimulus is salient and perceived very well by the participant since the relative direction is easily detected (Bingham 2004; Wilson et al. 2005; Wilson and Bingham 2008). The temporal stimulus on the other hand is less salient as the detection of relative direction is disrupted due to the absence of spatial information. Thus, increasing the saliency of the temporal stimulus, through the use of contrasting or complimentary colours, may reduce the differences observed between the two stimuli and allow for a more accurate comparison between them.

While the results for mean asynchrony were not significant they did show a tendency towards previous findings in the literature that used similar spatio-temporal stimuli. The data showed a tendency for participants to precede the stimulus at slower frequencies which is also found in other research (Buekers et al. 2000; Schmidt et al. 2007; Varlet et al. 2012) and follow the stimuli at faster frequencies again found in previous research (Schmidt et al. 2007; Varlet et al. 2012). The +20% temporal condition was extremely close to zero and participants tended to precede the stimulus instead of following it as was expected. The temporal -20% condition tended to precede the stimulus corresponding to the results from Varlet et al. (2012) for the same frequency and condition but the other two frequencies, preferred and +20% contrast the findings from Varlet et al. (2012). This may reflect the different eigenfrequencies of the pendulums used in our study (0.9 Hz) and Varlet et al. (2012) (0.75 Hz). Thus, the preferred frequency conditions in Varlet et al. (2012) were closer to the eigenfrequency of the pendulum, whereas the +20% conditions in the current article were closest to the eigenfrequency. The proximity of a given frequency to the eigenfrequency of the pendulum may have resulted in an improved ability to coordinate and thus explain the differences seen between the results of Varlet et al. (2012) and the present study.

The mean asynchrony for the temporal +20% condition reflects the tendency of the movement to arrive almost perfectly on time with the stimulus. This result is in contrast to the relatively high negative scores observed with the two other frequencies (-20% and preferred) for the temporal condition. This could be due to the inability of participants to perceive all the continuous information of the faster stimulus. The temporal +20% stimulus may be perceived more like flashes of a discrete visual signal. Coordination with discrete visual stimuli usually results in movements following the stimulus (Buekers et al. 2000; Varlet et al. 2012) and would allow for a possible explanation as to why the fastest temporal signal had a negative mean asynchrony that was extremely close to zero. The end points of the temporal stimuli are the dark black and bright green colours respectively. It is possible that this change in colour is more easily detected when the frequency is either slower than or at the preferred frequency. Finally, as previously mentioned the use of contrasting colours such as yellow and blue instead of the green and black may allow for enhanced detection of the colours during the experiment. While it is known from previous research that change in colour is perceived before motion (Cavanagh et al. 1984) further research is needed to investigate the perception of change in different colours over a range of frequencies.

The spatio-temporal condition clearly reduced the end point variability, which was significantly lower than the temporal stimulus. However, the absence of a difference between right and left end point anchoring could indicate the type of gaze strategy used by the participants. Roerdink et al. (2005) found that anchoring at the end points was not significantly different when participants fixated their gaze on the centre of a horizontally oscillating stimulus' amplitude or when they visually tracked the stimulus. Given the anchoring results presented in this article it is possible that participants used one or both of these strategies since there were no differences found between left and right anchoring across all conditions. Further research assessing the gaze strategies used by participants when coordinating with these types of visual stimuli is needed.

Overall, the results showing that synchronization significantly improved when spatial information was available appears to support the general theory of perception-action put forward by (Gibson 1986). Taking this Gibsonian approach the spatio-temporal stimulus appears to provide additional information, in the form of spatial information that appeared to improve the ability to synchronize movements with this stimulus. According to Gibson’s theory of perception-action the information picked up from our environment is meaningful and specific to the control of a given action (Kelso 1995). Thus, the information provided in the spatio-temporal stimulus provided more specific information related to the task compared to the temporal stimulus and as a consequence of this, synchronization improved. In this case the critical difference in the information provided by both stimuli was the spatial information, which created a congruency between the trajectory of the stimulus and the movement in the pendulum task. As previously mentioned the results relating to spatial anchoring appeared to in-directly support the theory put forward by Bingham (2004) which emphasises the importance of the information contained at the endpoints of a spatio-temporal stimulus. The significant improvement in spatial anchoring values with the spatio-temporal compared to temporal stimulus clearly support this theory showing that the presence of spatial information, specifically at the endpoints, helped to improve synchronization.

3.6 Conclusion

The results from this article have shown how important spatio-temporal information is for accurate perception of and coordination with a given visual stimulus. Often there appears to be a resilience of the motor system to adapt to changes in the environment. The data presented in this article identified that participants were still able to produce good levels of coordination when the amount of information was reduced and only temporal information was available. When the temporal stimulus was supplemented with spatial information the coordination improved significantly. As previously discussed, it is possible that the lower coordination values seen with the temporal stimuli are due to an inability of participants to perceive all the information provided. At the faster frequencies this stimulus may have been perceived more like flashes of a discrete rather than a continuous signal. From the results presented in this article it appears that participants can produce stable coordination without spatial information but that the supplementation of spatial information significantly improves coordination.

3.7 Funding source

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3.9 Link between Chapter 3 and Chapter 4

Purpose of Chapter 3:

The purpose of this chapter was to investigate the role of spatial information in synchronizing with visual stimuli. Participants were asked to synchronize wrist pendulum movements with temporal and spatio-temporal stimuli. The results indicated that the supplementation of spatial information in the spatio-temporal condition significantly improved the ability to synchronize with the stimuli. When information about relative direction was available, as with the spatio-temporal condition, coordination was significantly better. These results provide further support for previous research that has highlighted the important role perceiving relative direction has in motor coordination. Importantly, the lack of spatial information in the temporal condition did not result in a complete breakdown of synchronization. The lack of spatial information decreased the performance level but the synchronisation was still possible illustrating a resilience of the motor coordination system to adapt to changes in the environment.

Purpose of Chapter 4:

While chapter 3 clearly indicated that the presence of spatial information significantly improved synchronization with a visual stimulus, it remains unclear if the same supplementation of spatial information would also help stabilise coordination with an auditory stimulus. In order to address this question the following chapter assessed the ability of participants to synchronize movements with auditory or visual stimuli with temporal or spatio-temporal information available. Additionally, the second aspect of this study was to assess how multisensory integration of auditory and visual stimuli would be influenced by temporal and spatio-temporal information. In these bimodal conditions, participants were presented with audio-visual stimuli with different combinations of temporal and spatio-temporal information.

Chapter 4: Sensorimotor Synchronization with Audio-Visual Stimuli: Limited Multisensory Integration

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4.1 Abstract

Understanding how we synchronize our actions with stimuli from different sensory modalities plays a central role in helping to establish how we interact with our multisensory environment. Recent research has shown better performance with multisensory over unisensory stimuli, however the type of stimuli used has mainly been auditory and tactile. The aim of this article is to expand our understanding of sensorimotor synchronization with multisensory audio-visual stimuli and compare these findings to their individual unisensory counterparts. This research also aims to assess the role of spatio-temporal structure for each sensory modality. The visual and/or auditory stimuli had either temporal or spatio-temporal information available and were presented to the participants in unimodal and bimodal conditions. Globally, the performance was significantly better for the bimodal compared to the unimodal conditions, however this benefit was limited to only one of the bimodal conditions. In terms of the unimodal conditions, the level of synchronization with visual stimuli was better than auditory and while there was an observed benefit with the spatio-temporal compared to temporal visual stimulus this was not replicated with the auditory stimulus.

Key words: *sensorimotor synchronization; multisensory; audio-visual; spatio-temporal; anchoring*

4.2 Introduction

Through interaction with our environment the perceptual system detects essential information that supports us in organising our actions. Different strategies for synchronizing our actions with the environment are employed by the perceptual system. One such strategy involves maximizing the information from different modalities by integrating the relevant sensory information from the environment (Ernst and Bülthoff 2004). Research to date has provided a lot of understanding about how we synchronize our actions with auditory and visual stimuli when they are presented independently of each other yet there is a gap in the literature regarding how we integrate audio-visual information for synchronizing our actions. The current experiment aims to provide insight into sensorimotor synchronization with auditory and visual stimuli in both unimodal and bimodal conditions with different spatio-temporal structures.

It has been well established that auditory stimuli have high temporal saliency and visual stimuli high spatial saliency (Spence and Squire 2003; Ernst and Bülthoff 2004), thus the spatio-temporal structure of these modalities can influence their saliency. Research from the finger tapping literature using discrete stimuli has found better sensorimotor synchronization with auditory compared to visual stimuli (Repp 2005; Repp and Su 2013), indicating higher temporal saliency for auditory stimuli. Studies using visual stimuli have found that the addition of spatial information, for example a stimulus oscillating horizontally or vertically (spatio-temporal stimulus), improves synchronization compared to a stimulus containing only temporal information (Buekers et al. 2000; Hove et al. 2010; Armstrong et al. 2013). Additionally, the spatial saliency of visual stimuli is better than auditory stimuli (Ernst and Bülthoff 2004). Armstrong et al. (2013) specifically addressed the effect of modifying the spatio-temporal structure of a continuous visual stimulus and found that synchronization improved when spatial information was available. While the spatial saliency of auditory stimuli is lower than visual, supplementing this auditory stimulus with a spatial component could potentially improve the synchronization.

However, this has yet to be thoroughly investigated in the literature and is one of the aims of the current study.

While studies have focused extensively on sensorimotor synchronization with continuous visual stimuli to understand the perception-action dynamics (Zaal et al. 2000; Bingham et al. 2001; Bingham 2004; Kilner et al. 2007; Stanley et al. 2007; Lopresti-Goodman et al. 2008) much less emphasis has been placed on continuous auditory stimuli. Two recent articles have focused on comparing discrete and continuous auditory stimuli. Rodger & Craig (2011) found that while synchronization errors were smaller for discrete sounds, the stability of the synchronization was greater for continuous sounds. In contrast, Varlet et al. (2012), did not find any significant stability differences between their discrete and continuous auditory conditions. Given the limited number of studies addressing continuity with auditory stimuli further research is needed and the current study aims to add to this literature by assessing sensorimotor synchronization with continuous auditory stimuli.

It is also important to examine the possible spatio-temporal structural changes that may occur in movement when modifying the spatio-temporal structure of a stimulus. Anchoring, regions of reduced spatial or temporal variability in movement (Beek 1989), provides an appropriate analysis of how changes in the spatio-temporal structure of a stimulus can influence the variability in movement during a synchronization task. These local reductions can correlate to important task-specific information required for motor coordination (Beek 1989), which typically lie at the endpoints as shown with an oscillating visual stimulus (Hajnal et al. 2009). The analysis of differences between these left and right anchoring points can help in exploring the various factors that may influence sensorimotor synchronization. For example, Roerdink et al. (2008) investigated the effects of visual and musculoskeletal factors on anchoring using different gaze directions and wrist postures respectively. They found significant differences between left and right anchoring points revealing that both gaze direction and wrist posture can have a significant impact on the coordination dynamics. The importance of visual endpoints was supported by Armstrong et al. (2013) who found a significant increase in anchoring for an oscillating (spatial information) stimulus compared to a colour fading (no spatial information) stimulus. This highlights that while the continuous nature of a visual stimulus is important (see Varlet et al. 2012 for discussion) the supplementation of spatial information, e.g. in the oscillating stimulus, is key for stabilising synchronization. The use of anchoring with auditory stimuli in the current study is novel and could potentially provide useful insight into the task-specific information that is utilised by the perceptual system in coordination with this modality.

Much of the research on multisensory synchronization has stemmed from the tapping literature and, as a consequence of this, focused on the integration of tactile and auditory stimuli. Tactile stimulation is closely related to the task of finger tapping given that one of the discrete points of the movement, flexion, often corresponds to a tap on a surface. All of these studies have reported evidence of multisensory integration and a benefit in terms of synchronization when compared to the unimodal conditions (Kelso et al. 2001; Wing et al. 2010; Elliott et al. 2010; Zelic et al. 2012). Few studies have reported utilising auditory and visual stimuli although two recent studies have provided some novel insight into synchronization with these types of stimuli, both of which provided clear evidence of a bimodal benefit in terms of synchronization. Elliott et al. (2010) investigated finger tapping synchronization with a range of conditions, one of which was a bimodal audio-visual discrete stimulus. Their results indicated that the bimodal audio-visual condition produced significantly better synchronization compared to the unimodal auditory and visual conditions. Similarly, Varlet et al. (2012) provided novel evidence for enhanced synchronization with bimodal audio-visual stimuli presented in both discrete and continuous modes.

The main aim of this current paper is to build on the findings from Varlet et al. (2012) using similar methodology with continuous stimuli, i.e. the fading square and frequency-modulated sound. Using these stimuli the current study will assess the effect of spatio-temporal structure on synchronization as well as the effect of frequency as participants will synchronize pendulum movements at their preferred and ±20% of their preferred frequency. Research has shown that participants tend to produce a movement frequency that is slightly faster than the eigenfrequency of the pendulum (Schmidt et al. 2007; Richardson et al. 2008). Considering that individual variability is inevitable between participants the use of the individual participants preferred frequency in the current study accommodates this variability in movement frequency and ensures that each participant is synchronizing at a preferred and ±20% of preferred frequency that is specific to them.

Armstrong et al. (2013) found that synchronization with continuous visual stimuli was significantly improved when spatial information was available (horizontally oscillating square, i.e. spatial and temporal information) compared to a temporal stimulus (fading square, i.e. only temporal information). It is expected that for the unimodal conditions the effect observed by Armstrong et al. (2013) for visual stimuli will be diminished with the auditory conditions due to the poor spatial saliency of this modality. Thus, it is hypothesised that for the auditory conditions the performance in the synchronization task will be similar for the temporal and spatio-temporal stimuli while for the visual conditions it is hypothesised that the findings will support those from Armstrong et al. (2013). Based on the multisensory research discussed above it appears that there is a bimodal benefit in terms of synchronization, indicating a significant improvement in synchronization performance when a multisensory stimulus compared to a unisensory stimulus is available. Based on this evidence it is hypothesised that the bimodal conditions will produce significantly better performance than the unimodal conditions. It is also hypothesised that within these multisensory conditions the synchronization task will be significantly better when spatio-temporal information is available in both modalities compared to when temporal information is available in one or both modalities. This hypothesis is based on the concept that the spatial information being provided is congruent with the movement in the synchronization task and should provided additional information for the participants that will allow them to perform the task better.

4.3 Methodology

4.3.1 Participants

Twelve volunteers (five females and seven males) between the ages of 18 and 42 years (25.58 yrs. ±6.72) took part in the experiment. All participants were right handed, had normal or corrected to normal vision and no known history of a neuromuscular deficit that would affect their participation. Colour blindness was assessed using a series of Ishihara pictures and none of the participants had any form of colour blindness. No compensation was given to the participants for their involvement in the experiment. Ethical approval was received from the Dublin City University Research Ethics Committee (DCUREC/2011/038).

4.3.2 Stimuli

There were a total of 8 different stimuli in this experiment, 4 Unimodal base stimuli and 4 Bimodal stimuli. The various stages of the four base stimuli are displayed in Fig. 1. A screen (Dell Trinitron Ultrascan 1600HS Series CRT Monitor, Model D1626HT) displayed the visual stimuli and was placed at eye level approximately 1 m from the participants. These visual stimuli consisted of two different oscillating visual signals presented on a screen with a grey background and were similar to the stimuli used by Armstrong et al. (2013). The temporal visual stimulus (Visual Centred – VC, i.e. containing only temporal information) appeared as a stationary square (5.2 × 5.2 cm) in the centre of the screen that continuously faded between a red and yellow colour in a sinusoidal fashion (Fig. 1a). The spatio-temporal visual stimulus (Visual Panning – VP, i.e. containing both spatial and temporal information) appeared as a square (5.2 × 5.2 cm) oscillating horizontally across the screen in a sinusoidal fashion with an amplitude of 28 cm while also oscillating in a sinusoidal fashion between a red and yellow colour (Fig. 1b). The red colour was clearest when the square reached the left endpoint and the yellow colour was clearest when it reached the right endpoint on screen (Fig. 1b). Both of these visual stimuli were created in Matlab using the Psychophysics Toolbox extensions (Pelli 1997; Brainard 1997; Kleiner et al. 2007).

The auditory stimuli were presented through noise cancelling headphones and consisted of a continuous tone that modulated from a low pitch (400 Hz) to a high pitch (800 Hz) in a sinusoidal fashion. The temporal auditory stimulus (Auditory Centred – AC, i.e. containing only temporal information) was the frequency-modulated tone that was balanced in both ears (Fig. 1c). The spatio-temporal auditory stimulus (Auditory Panning – AP, i.e. containing both spatial and temporal information) consisted of the same frequency-modulated tone with an added spatial component that panned the sound between left and right ear during each oscillation (Fig. 1d). The high pitch was always heard on the left and the low pitch was always heard on the right. Both auditory stimuli were created using Supercollider (McCartney 2002).

The Bimodal conditions consisted of the different possible combinations of the two visual and two auditory stimuli described above: Auditory Centred and Visual Centred (AC-VC), Auditory Panning and Visual Centred (AP-VC), Auditory Centred and Visual Panning (AC-VP) and Auditory Panning and Visual Panning (AP-VP). Data was recorded at 100 Hz using a Measurement Computing Data Acquisition Device (Measurement Computing, USB-1608FS) and stored for further analysis. Data collection and the presentation of all stimuli were controlled in Matlab using the Psychophysics Toolbox extensions (Pelli 1997; Brainard 1997; Kleiner et al. 2007).

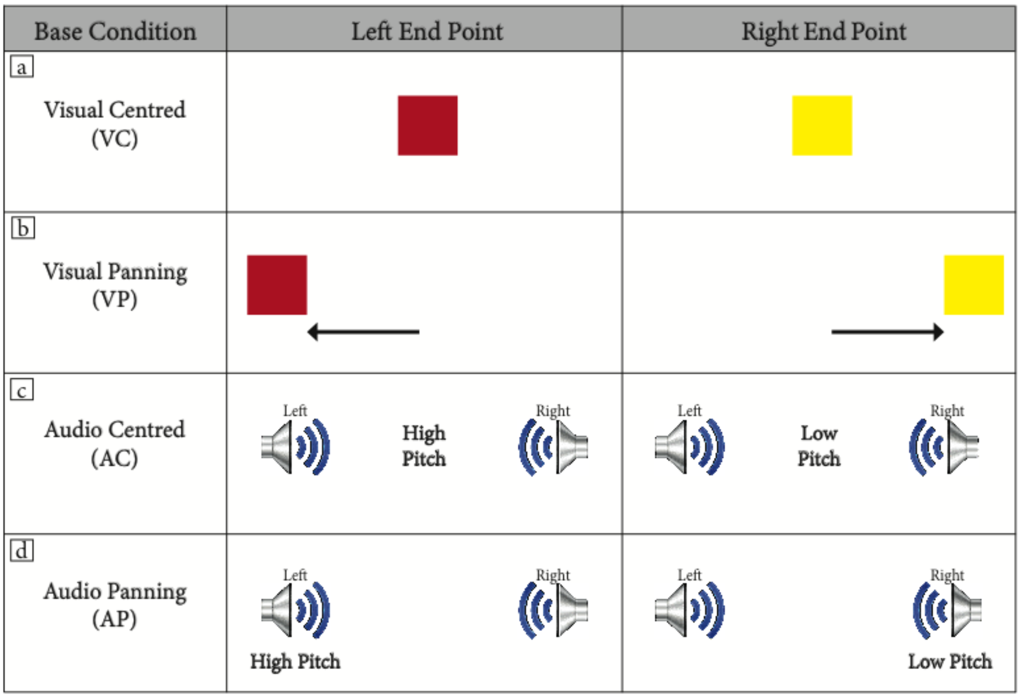

Figure 1 Stages of the four unimodal base stimuli. (a) For the first condition VC, the colour of the square transitions from red to yellow with red corresponding to the left endpoint and yellow to the right endpoint. (b) VP is an oscillating square with the left endpoint of the square corresponding to the left endpoint of the movement and the right endpoint of the square with the right endpoint of the movement. The colour of the square also changes in exactly the same way as VC with red as the left endpoint and yellow as the right endpoint (c) AC is a frequency-modulated tone that is balanced in both ears with the high pitch corresponding to the left endpoint of the participant's movement and the low pitch corresponding to the right endpoint of the movement. (d) AP is the same tone but with an added pan that moves the sound. The left endpoint corresponds to a high pitch that is only heard in the left ear, the sound then travels to the right ear where the low pitch corresponds to the right endpoint.

4.3.3 Procedure

Upon arrival participants were handed an information sheet about the experiment and were asked to sign an informed consent form. Following this, the experiment was explained in three parts, 1) preferred frequency calculation, 2) familiarisation and 3) experimentation. Participants sat in a height adjustable chair with a forearm support and gripped an aluminium pendulum with their right hand. The pendulum was 49 cm long with a weight of 53 g attached at the end of the rod. Its eigenfrequency was 0.75 Hz. Participants were prevented from viewing the pendulum's movements with a wooden cover and the arm of the participant was also concealed using a sliding panel. Participants swung the pendulum in a darkened room, through the frontal plane by pronating and supinating their forearm and were told to move the pendulum with an amplitude of 45 degrees to the right and 45 degrees to the left from the resting position of the pendulum. An example of the experimental setup is shown in Figure 2. For the preferred frequency calculation participants were asked to swing the pendulum in a dark room for two minutes at a pace that was ‘most comfortable’ for them. The preferred frequency of each participant was used to create two additional frequencies: +20% of preferred and -20% of preferred.

During the familiarisation stage, participants were required to synchronize the movements of the handheld pendulum with each of the eight conditions. The exact instructions for synchronization were the same as in the experimentation stage and are described below. The stimuli were each presented once and at each participant’s preferred frequency. Additional presentations of the stimuli were provided if required by the experimenter in order to ensure an understanding of the different experimental conditions. For the VC condition, participants had to swing the handheld pendulum synchronizing the left endpoint of the pendulum swing with the brightest red and the right endpoint with the brightest yellow (Fig. 1a). Similarly, for the VP condition, participants had to swing to the left as the square moved left fading to a red colour and to the right as the square moved right fading to a yellow colour, synchronizing the endpoint of the movements with the square’s endpoints (Fig. 1b). For the AC condition, participants were required to synchronize the left endpoint of the pendulum swing with the high pitch and the right endpoint with the low pitch (Fig. 1c). For the AP condition, participants were required to swing the pendulum to the left as the sound panned to the left ear with a high pitch and to the right as the sound panned to the right ear with a low pitch, synchronizing the endpoint of the movements with the sounds endpoints (Fig. 1d).

One block of the experiment consisted of three frequencies (Preferred, +20% and -20%) and the eight stimuli discussed previously, resulting in a total of 24 conditions. Participants completed one trial of each of the 24 randomised conditions for each of the three blocks. There was a 30 second break after each 40 second trial and a five minute break between blocks.

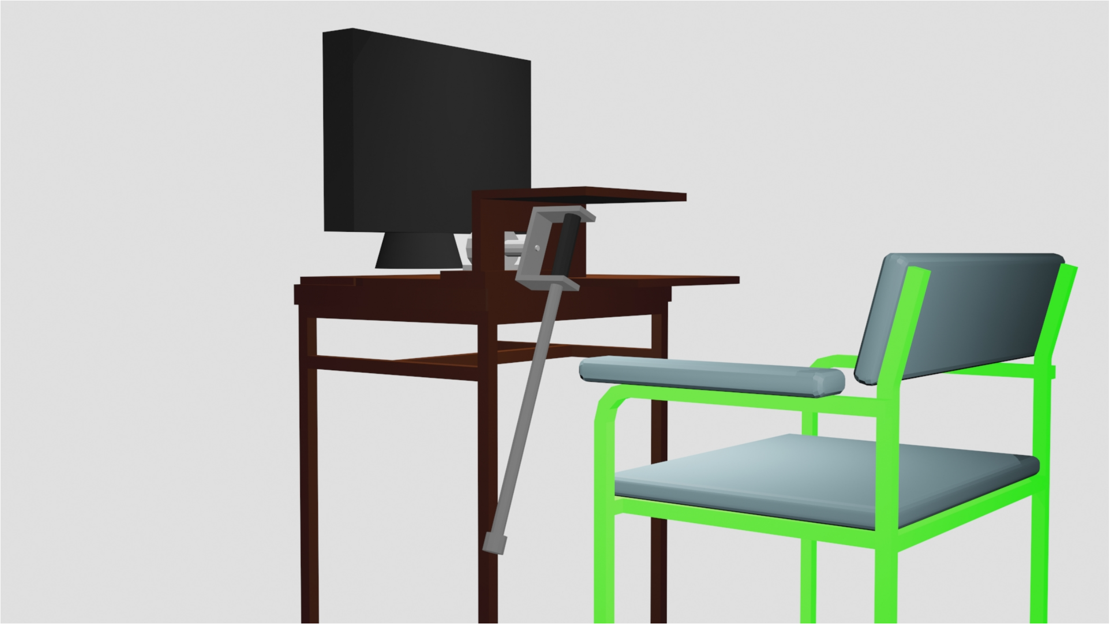

Figure 2 Example of experimental setup

4.3.4 Data reduction

The two main variables used to assess synchronization performance were continuous relative phase (CRP) and the standard deviation of CRP (SD CRP), both of which provide a detailed view of coordination between the participant's movements and that of the stimuli as well as the variability of this coordination. Before any analysis the first 10 seconds of data were removed and the remaining 30 seconds were low pass filtered using a 10 Hz Butterworth filter. Data were then normalised between ±1 using min max scaling. All data were averaged across each of the three trials for the 24 experimental conditions. In order to assess the degree of coordination between the participant and the stimulus CRP was assessed. CRP was calculated using a Hilbert Transform and scaled between 0° and 180°. The first and last cycles of each trial were removed due to distortions caused by the Hilbert Transform during the computation of relative phase (Pikovsky et al. 2003). Based on these CRP values the SD CRP was calculated, which allowed for an assessment of the variability of coordination. In order to determine the lead/lag nature of the participant's movement in relation to the stimulus the average CRP at the endpoints of the stimulus was calculated using a range of ±180˚, negative values indicate participants lead the stimulus while positive values indicate participants lag the stimulus.

In order to examine any reductions in spatial or temporal variability at the endpoints of the movement, anchoring was calculated. We analysed the spatial anchoring using the SD of the participant's movement at the endpoints of their pendulum swing (SD in arbitrary units). Temporal anchoring constituted the variability in the asynchrony between the stimulus arrival time at an endpoint and the corresponding time of the participant's arrival (SD in ms). A low value for either of these anchoring variables indicates a reduction in the variability at the endpoint of the movement. The anchoring data were divided into two categories, right and left endpoint of the movement. The Spatial and Temporal Anchoring Index, $\mathrm{AI}_{\mathrm{spatial}}$ and $\mathrm{AI}_{\mathrm{temporal}}$ respectively, were then calculated using the following equation (Roerdink et al. 2008):

$$\mathrm{AI} = \frac{\mathrm{SD}_l}{\mathrm{SD}_l + \mathrm{SD}_r},$$

where SD_l and SD_r represent the spatial or temporal anchoring at the left and right endpoints respectively. An anchoring index of 0.5 indicates that the anchoring is the same on the left and right. A value less than 0.5 indicates more anchoring on the left than the right and a value greater than 0.5 indicates more anchoring on the right than the left.

4.3.5 Statistical analysis

All the statistical analysis was performed using SPSS (IBM SPSS Statistics 20) using the averaged data across the three trials and the twelve participants. Several repeated-measures analysis of variance (ANOVA) were used to analyse CRP, SD CRP, $\mathrm{AI}_{\mathrm{spatial}}$ and $\mathrm{AI}_{\mathrm{temporal}}$. A comparison between unimodal and bimodal conditions was conducted using repeated-measures ANOVAs with Stimulus Frequency (Preferred, +20% and -20%) and Stimulus Mode (Unimodal and Bimodal) as factors. In order to understand the effect of sensory modality and spatio-temporal integration, repeated-measures ANOVAs were preformed on the unimodal conditions with Stimulus Frequency (Preferred, +20% and -20%), Stimulus Modality (Visual and Auditory) and Stimulus Type (Centred and Panning) as factors. We then investigated the effect of sensory integration with the different combinations of auditory and visual stimuli in the bimodal conditions. This was assessed using repeated-measures ANOVAs with Stimulus Frequency (Preferred, +20% and -20%) and Stimulus Combination (AC-VC, AP-VC, AC-VP and AP-VP) as factors.

Sphericity was assessed for each of these variables and the Greenhouse and Geisser's correction for the degrees of freedom was applied when sphericity was not met. Post Hoc analysis using Bonferroni's correction was used where necessary in order to detail the direction of significant effects. One-sample *t*-tests were used to assess the differences from zero of the average CRP (scaled to ±180°). Additionally, $AI_{spatial}$, and $AI_{temporal}$ were also assessed using one-sample *t*-tests to see whether the anchoring index differed significantly from 0.5, which would indicate more anchoring at one of the two endpoints. Data were averaged for each of the following categories to assess their individual effects on anchoring: Unimodal Centred, Unimodal Panning, all four bimodal conditions (AC-VC, AP-VC, AC-VP, AP-VP) and all three frequency conditions (Preferred, +20% and -20%). The size of the effect for all of the ANOVA analysis was reported by means of the partial eta squared (η^2_p).

4.4 Results

4.4.1 Mean Continuous Relative Phase

The 3 (Stimulus Frequency) × 2 (Stimulus Mode) repeated-measures ANOVA on CRP yielded a significant main effect for Stimulus Mode ($F_{1, 11} = 4.894$, $P < .05$, $\eta^2_p = .31$), revealing higher CRP values, which indicates lower synchronization performance, in the Unimodal (24.8°) compared to Bimodal (22.5°) conditions, as shown in Fig. 3. There was also a significant main effect for Stimulus Frequency ($F_{2, 22} = 7.460$, $P < .01$, $\eta^2_p = .40$), which showed higher CRP values with the Preferred (25.5°) and -20% (26.7°) conditions compared to +20% (18.8°). The interaction between Stimulus Frequency and Stimulus Mode was not found to be significant, ($F_{2, 22} = 0.136$, $P > .05$, $\eta^2_p = .01$). One-sample *t*-tests revealed that CRP was significantly different from zero for all Stimulus frequencies; Preferred ($M = -15.6°$; $SD = 18.8°$) ($t(11) = 2.88$, $P < .05$), +20% ($M = -8.5°$; $SD = 11.0°$) ($t(11) = 2.67$, $P < .05$) and -20% ($M = -18.13°$; $SD = 16.0°$) ($t(11) = 3.94$, $P < .01$). This indicated that participants tended to lead the stimulus for all frequencies.

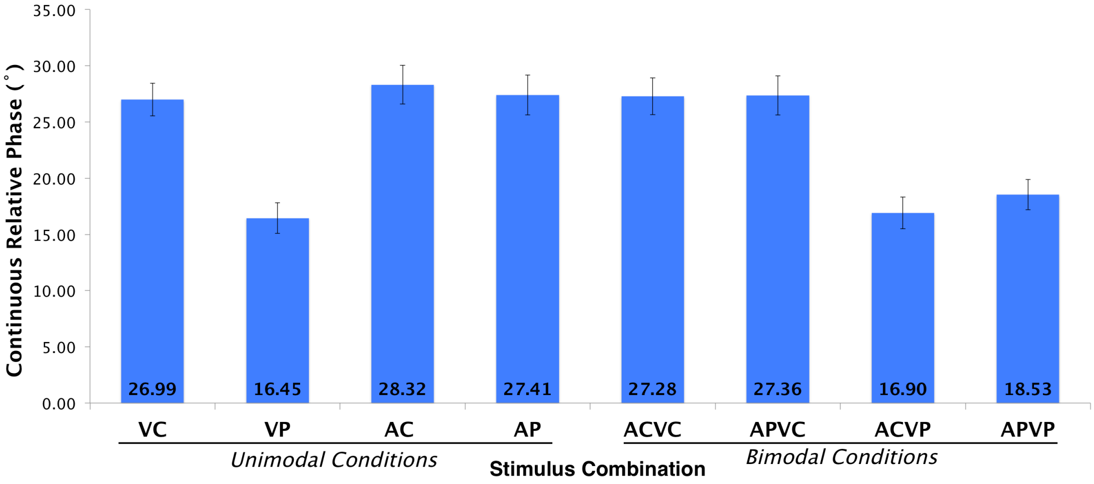

Figure 3 Continuous Relative Phase means for all conditions

For the unimodal conditions, the 3 (Stimulus Frequency) × 2 (Stimulus Modality) × 2 (Stimulus Type) repeated-measures ANOVA produced significant main effects for Sensory Modality ($F_{1,11} = 7.23$, $P < .05$, $\eta^2_p = .40$), indicating that significantly higher CRP values were present in the Auditory (27.9°) compared to the Visual (21.7°) conditions. There was also a significant main effect for Stimulus Frequency ($F_{2,22} = 8.93$, $P < .01$, $\eta^2_p = .45$), which supported the Stimulus Frequency findings mentioned previously and a significant main effect for Stimulus Type ($F_{1,11} = 28.54$, $P < .01$, $\eta^2_p = .72$), indicating higher CRP values for the Centred (27.7°) compared to the Panning (21.9°) conditions. The interaction between Sensory Modality and Stimulus Type was found to be significant ($F_{1,11} = 22.58$, $P < .01$, $\eta^2_p = .62$), a simple effects analysis revealed that CRP was significantly reduced for the Panning compared to the Centred unimodal conditions but only with the Visual stimulus ($P < .01$). The interaction between Sensory Modality and Frequency was also found to be significant ($F_{2,22} = 4.49$, $P < .05$, $\eta^2_p = .29$), a simple effects analysis revealed that CRP was significantly higher in the -20% compared to the Preferred and +20% visual conditions ($P < .05$), while CRP was significantly lower in the +20% compared to Preferred and -20% auditory conditions ($P < .05$). No other significant interactions were found with this ANOVA; Stimulus Type and Frequency ($F_{2,22} = 0.54$, $P > .05$, $\eta^2_p = .03$), Stimulus Type, Sensory Modality and Frequency ($F_{2,22} = 0.36$, $P > .05$, $\eta^2_p = .03$). One-sample *t*-tests revealed significant differences from zero for both Unimodal Centred stimuli ($t(11) = 2.95$, $P < .05$) and Unimodal Panning stimuli ($t(11) = 3.11$, $P < .01$). This indicated that participants tended to lead the stimulus when it was Centred ($M = -13.3°$; $SD = 15.7°$) and Panning ($M = -12.1°$; $SD = 13.4°$).

For the bimodal conditions, the 3 (Stimulus Frequency) × 4 (Stimulus Combination) repeated-measures ANOVA yielded a significant main effect for Stimulus Frequency ($F_{2,22} = 5.40$, $P < .05$, $\eta^2_p = .33$), which indicated that CRP was significantly higher for the -20% (25.4°) compared to +20% (17.8°) conditions and a significant main effect for Stimulus Combination ($F_{1.59,17.53} = 27.76$, $P < .01$, $\eta^2_p = .72$), displaying a reduction in CRP values for AP-VP (18.5°) and AC-VP (16.9°) compared to AC-VC (27.3°) and AP-VC (27.4°). There was no significant interaction found between Stimulus Frequency and Stimulus Combination ($F_{6,66} = 1.07$, $P > .05$, $\eta^2_p = .09$). The one-sample *t*-tests revealed significant differences from zero for all of the four bimodal conditions; AC-VC ($t(11) = 3.76$, $P < .01$), AP-VC ($t(11) = 3.23$, $P <$

.01), AC-VP (*t*(11) = 3.81, *P* < .01) and AP-VP (*t*(11) = 4.47, *P* < .01), indicating that participants tended to lead the stimulus. Table 1 displays the one-sample *t*-tests results for CRP (scaled to ±180°).

Categories	Mean	SD	t	df	Sig (2-tailed)
Unimodal Centered	-12.07	13.44	3.11	11	.010
Unimodal Panning	-13.33	15.66	2.95	11	.013
ACVC	-18.40	16.96	3.76	11	.003
APVC	-17.77	19.06	3.23	11	.008
ACVP	-11.66	10.62	3.81	11	.003
APVP	-13.93	10.81	4.47	11	.001
Preferred Freq	-15.58	18.75	2.88	11	.015
+20% Freq	-8.50	11.03	2.67	11	.022
-20% Freq	-18.13	15.96	3.94	11	.002

Table 1 CRP one-sample *t*-tests

4.4.2 Standard Deviation of Continuous Relative Phase

The 3 (Stimulus Frequency) × 2 (Stimulus Mode) repeated-measures ANOVA on SD CRP yielded a significant main effect for Stimulus Mode ($F_{1,11} = 55.75$, $P < .01$, $\eta^2_p = .84$), indicating higher SD CRP in the Unimodal (12.3°) compared to Bimodal (10.6°) conditions, see Fig. 4 for the mean SD CRP of all conditions. There was also a significant main effect for Stimulus Frequency ($F_{2,22} = 6.81$, $P < .01$, $\eta^2_p = .38$), indicating lower SD CRP with +20% (10.6°) compared to -20% (12.7°) conditions. The interaction between Stimulus Frequency and Stimulus Mode was not found to be significant ($F_{2,22} = .14$, $P > .05$, $\eta^2_p = .01$). In order to understand where these differences between the unimodal and bimodal conditions lay, an additional 3 (Stimulus Frequency) × 8 (Condition) ANOVA was conducted which compared each condition against the other seven conditions. The most interesting finding from this analysis related to the significant effect of Condition ($F_{7,77} = 44.36$, $P < .01$, $\eta^2_p = .80$); AC-VC (11.90°) had significantly lower SD CRP compared to its unimodal counterparts, VC (13.89°) and AC (13.94°).

For the unimodal conditions, the 3 (Stimulus Frequency) × 2 (Stimulus Modality) × 2 (Stimulus Type) repeated-measures ANOVA on the SD CRP produced significant main effects for Sensory Modality ($F_{1,11}$ = 32.54, P < .01, η^2_p = .75) and Stimulus Type ($F_{1,11}$ = 54.09, P < .01, η^2_p = .83), which all supported the previous analysis with CRP. A significant main effect for Stimulus Frequency ($F_{2,22}$ = 7.48, P < .01, η^2_p = ..41) was also found which indicated lower SD CRP values with the +20% (11.4°) compared to -20% (13.6°) conditions. The interaction between Sensory Modality and Stimulus Type was found to be significant ($F_{1,11}$ = 24.09, P < .01, η^2_p = .69), a simple effects analysis revealed that SD CRP was significantly reduced for the Panning compared to the Centred unimodal conditions but only for the Visual stimulus (P < .01). No other significant effects were found with this ANOVA; Sensory Modality and Frequency ($F_{2,22}$ = 1.34, P > .05, η^2_p = .11), Stimulus Type and Frequency ($F_{2,22}$ = 0.61, P > .05, η^2_p = .05), Sensory Modality, Stimulus Type and Frequency ($F_{2,22}$ = 0.02, P > .05, η^2_p = .00).

For the bimodal conditions, the 3 (Stimulus Frequency) × 4 (Stimulus Combination) repeated-measures ANOVA on SD CRP yielded significant findings for Stimulus Combination ($F_{3,33}$ = 53.90, P < .01, η^2_p = .83), revealing that both AC-VP (8.6°) and AP-VP (9.3°) had lower SD CRP compared to AC-VC (11.9°) and AP-VC (12.8°). Stimulus Frequency was not found to be significant ($F_{2,22}$ = 3.37, P > .05, η^2_p = .23). There was no significant interaction found between Stimulus Frequency and Stimulus Combination ($F_{6,66}$ = 1.00, P > .05, η^2_p = .08).

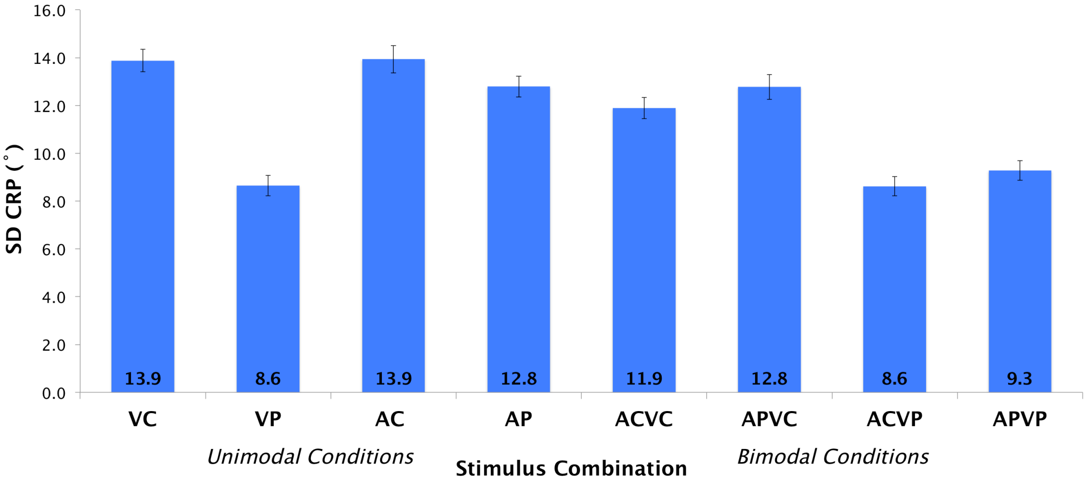

Figure 4 Standard Deviation of Continuous Relative Phase for all Conditions

4.4.3 Spatial Anchoring

For the 3 (Stimulus Frequency) × 2 (Stimulus Mode) repeated measures ANOVA no significant effects were found; Stimulus Mode ($F_{1,11} = 0.04, P > .05, \eta^2_p = .00$), Stimulus Frequency ($F_{2,22} = 0.39, P > .05, \eta^2_p = .03$), Stimulus Mode and Stimulus Frequency interaction ($F_{2,22} = 0.82, P > .05, \eta^2_p = .07$). For the 3 (Stimulus Frequency) × 2 (Stimulus Modality) × 2 (Stimulus Type) repeated measures ANOVA no significant effects were found; Sensory Modality ($F_{1,11} = 3.00, P > .05, \eta^2_p = .21$), Stimulus Type ($F_{1,11} = 1.19, P > .05, \eta^2_p = .10$), Stimulus Frequency ($F_{2,22} = 0.02, P > .05, \eta^2_p = .00$), Sensory Modality and Stimulus Type interaction ($F_{1,11} = 0.27, P > .05, \eta^2_p = .02$), Sensory Modality and Stimulus Frequency interaction ($F_{2,22} = 0.03, P > .05, \eta^2_p = .00$), Stimulus Type and Frequency interaction ($F_{2,22} = 0.08, P > .05, \eta^2_p = .01$), Sensory Modality, Stimulus Type and Stimulus Frequency interaction ($F_{2,22} = 2.94, P > .05, \eta^2_p = .21$). For the 3 (Stimulus Frequency) × 4 (Stimulus Combination) repeated-measures ANOVA no significant effects were found; Stimulus Combination ($F_{3,33} = 1.31, P > .05, \eta^2_p = .11$), Stimulus Frequency ($F_{2,22} = 1.18, P > .05, \eta^2_p = .10$), Stimulus Combination and Stimulus Frequency interaction ($F_{6,66} = 0.74, P > .05, \eta^2_p = .06$). Similarly none of the one-sample *t*-tests performed on $AI_{spatial}$ indicated significant differences from zero, table 2 displays the one-sample *t*-tests results for $AI_{spatial}$. The lack of any significant findings for this variable indicates that the variability of movement at the left and right endpoints of the pendulum swing were similar across all conditions. Figure 5 displays the mean Spatial Anchoring values for all conditions.

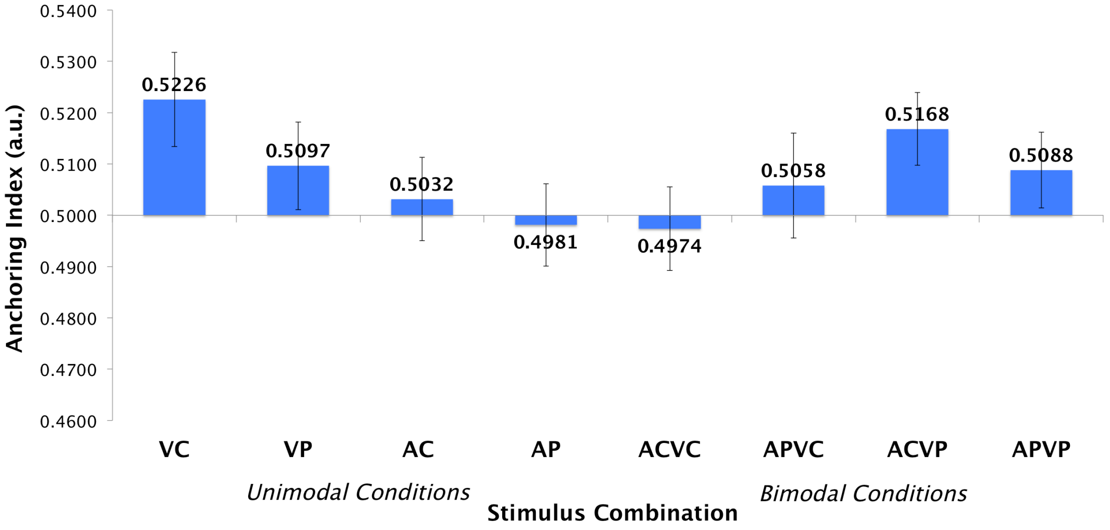

Figure 5 Mean Spatial Anchoring Index values for all conditions

Categories	Mean	SD	t	df	Sig (2-tailed)
Unimodal Centered	.50	.03	.47	11	.646
Unimodal Panning	.51	.03	1.47	11	.170
ACVC	.50	.03	-.28	11	.784
APVC	.51	.02	.82	11	.427
ACVP	.52	.03	1.80	11	.099
APVP	.51	.05	.62	11	.548
Preferred Freq	.51	.03	.75	11	.469
+20% Freq	.51	.03	1.67	11	.124
-20% Freq	.50	.04	.302	11	.768

Table 2 $AI_{Spatial}$ one-sample *t*-tests

4.4.4 Temporal Anchoring

$AI_{temporal}$ was initially analysed using a 3 (Stimulus Frequency) × 2 (Stimulus Mode) repeated-measures ANOVA which yielded no significant main effects; Stimulus Mode ($F_{1,11} = 1.51$, $P > .05$, $\eta^2_p = .12$), Stimulus Frequency ($F_{2,22} = 0.50$, $P > .05$, $\eta^2_p = .04$), Stimulus Mode and Stimulus Frequency interaction ($F_{2,22} = 2.26$, $P >$

.05, η^2_p = .17). The one-sample *t*-test focusing on Unimodal and Bimodal conditions revealed that Unimodal conditions (*M* = .4959; *SD* = .0055) differed significantly from 0.5 (*t*(11) = -2.55, *P* < .05), which indicates that these conditions had more temporal anchoring at the left endpoint compared to the right. The one-sample *t*-test, which assessed the effect of Frequency on all conditions, revealed that the Preferred conditions (*M* = .4959; *SD* = .0063) had an anchoring index significantly different from 0.5 (*t*(11) = -2.23, *P* < .05), indicating that there was more temporal anchoring at the left endpoint than the right endpoint for these conditions.

For the Unimodal conditions, the 3 (Stimulus Frequency) × 2 (Stimulus Modality) × 2 (Stimulus Type) repeated-measures ANOVA found a significant interaction between Stimulus Type and Stimulus Frequency ($F_{2,22}$ = 4.28, P < .05, η^2_p = .28). A simple effects analysis revealed a significantly lower Temporal Anchoring Index for Preferred compared to +20% visual conditions. No other significant effects were found; Sensory Modality ($F_{1,11}$ = 0.29, P > .05, η^2_p = .03), Stimulus type ($F_{1,11}$ = 0.02, P > .05, η^2_p = .00), Stimulus Frequency ($F_{2,22}$ = 0.98, P > .05, η^2_p = .08), Sensory Modality and Stimulus Type interaction ($F_{1,11}$ = 0.80, P > .05, η^2_p = .07), Sensory Modality and Stimulus Frequency interaction ($F_{2,22}$ = 3.09, P > .05, η^2_p = .22), Sensory Modality, Stimulus Frequency and Stimulus Type interaction ($F_{2,22}$ = 0.16, P > .05, η^2_p = .01). The one-sample *t*-test, which assessed the four base Unimodal conditions, found that AP (*M* = .4943; *SD* = .0050) was significantly different from 0.5. AP (*t*(11) = -3.99, *P* < .01) produced more temporal anchoring on the left compared to the right endpoint.

For the Bimodal conditions, the 3 (Stimulus Frequency) × 4 (Stimulus Combination) repeated-measures ANOVA yielded no significant findings; Stimulus Combination ($F_{3,33}$ = 0.60, P > .05, η^2_p = .05), Stimulus Frequency ($F_{2,22}$ = 1.43, P > .05, η^2_p = .12), Stimulus Combination and Stimulus Frequency interaction ($F_{6,66}$ = 0.27, P > .05, η^2_p = .02). The one-sample *t*-test, which assessed the four Bimodal conditions, found that none of the conditions differed significantly from 0.5. The $AI_{temporal}$ values for all conditions are presented in Fig. 6. Table 3 displays the one-sample *t*-tests results for $AI_{temporal}$.

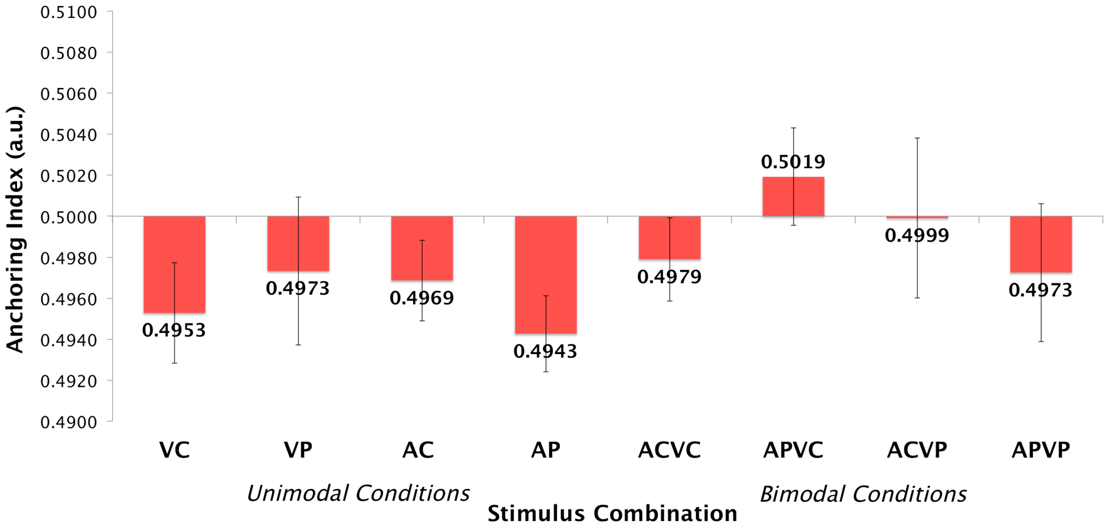

Figure 6 Mean Temporal Anchoring Index values for all conditions

Categories	Mean	SD	t	df	Sig (2-tailed)
Unimodal Centered	.50	.01	-2.00	11	.071
Unimodal Panning	.50	.01	-2.29	11	.043
ACVC	.50	.01	-.92	11	.377
APVC	.50	.01	.98	11	.349
ACVP	.50	.01	-.02	11	.983
APVP	.50	.02	-.61	11	.556
Preferred Freq	.50	.01	-2.23	11	.047
+20% Freq	.50	.01	-.86	11	.409
-20% Freq	.50	.01	-.45	11	.663

Table 3 $\mathrm{AI}_{\mathrm{Temporal}}$ one-sample *t*-tests

4.5 Discussion

The current study aimed at assessing whether auditory and visual stimuli can be integrated to produce stable synchronization and if the spatio-temporal structure of the stimuli affects this integration. For the unimodal stimuli the results indicated better synchronization with visual compared to auditory stimuli. When spatial information was supplemented to these unisensory conditions a significant improvement in synchronization was found with the visual stimuli supporting previous findings from Armstrong et al. (2013). However, the same effect was not observed with the auditory stimuli. Interestingly, there was only a limited benefit for the bimodal compared to unimodal conditions.

In the past, research has shown that auditory stimuli help stabilise synchronization better than visual stimuli (Repp 2005; Repp and Su 2013) however most of the research has used an event-based task which typically rely heavily on temporal timing (i.e. finger tapping). A recent study assessing the continuity of stimuli found that synchronization stability was significantly improved for continuous compared to discrete conditions but only for the visual and not the auditory stimuli (Varlet et al., 2012). The results of the current study indicated novel evidence for better and more stable synchronization with visual compared to auditory stimuli of a continuous nature, which emphasises the preference of the perceptual system for continuous information with visual stimuli. However, continuous auditory stimuli, even with additional spatial information, do not appear to improve synchronization. More generally the results also confirmed previously well established findings, participants tended to lead the continuous stimuli (Buekers et al. 2000; Schmidt et al. 2007; Varlet et al. 2012).

While there was a significant improvement in synchronization when spatial information was available in the unimodal conditions this was limited to the visual stimuli, as revealed by the interaction between Sensory Modality and Stimulus Type for CRP. These results support the findings from Armstrong et al. (2013) relating to visual stimuli and provide novel evidence that the supplementation of spatial information with a continuous auditory stimulus did not significantly improve synchronization with a continuous task. These findings may not be surprising given the dominance of auditory stimuli in the temporal domain and the lack of major differences between the discrete and continuous auditory stimuli in terms of synchronization stability in Varlet et al. (2012). In contrast, Rodger & Craig (2011) provided an interesting comparison between discrete and continuous auditory stimuli with spatial information available in both conditions. Their continuous stimulus seemed to provide essential information between taps that helped stabilise the synchronization more than the discrete stimulus. These contrasting findings could imply that spatial information affects synchronization differently depending on the nature of the task. Additionally, perhaps the nature of the auditory stimulus itself may also affect synchronization since the stimulus used in Rodger and Craig (2011) had a more salient event boundary compared to that used in Varlet et al. (2012) suggesting that further research comparing these different auditory stimuli is warranted.

The saliency of particular parts of a stimulus is essential in understanding how the perception-action coupling is controlled in motor coordination. It has been highlighted using the Perceptually Driven Dynamical model for motor coordination (Bingham 2004) that relative direction plays a key role in the saliency of a visual stimulus, with the endpoints of an oscillating visual stimulus presenting the most salient and task-relevant information for synchronization (Hajnal et al. 2009). The results from the current study appear to indicate similar salient points in one of the auditory conditions. There was significantly more temporal anchoring on the left compared to the right endpoint of participants' movement for the AP conditions suggesting that the left endpoint of this stimulus, 800 Hz, was more salient than the right, 400 Hz. This phenomenon has been extensively investigated and has been found to be a general effect when discriminating or synchronizing with frequency modulated auditory stimuli (Demany and McAnally 1994; Cheveigné 2000; McAnally 2002). In these studies, across a wide range of frequencies, participants consistently found that the peak element of the auditory sound (high frequency) was more salient than the trough (low frequency). While the anchoring results relating to the auditory stimulus clearly provide some support for the model of motor coordination proposed by

Bingham, importantly the results also highlight the importance of the saliency of these endpoints since the high frequency endpoint, 800 Hz, had more anchoring than the low frequency, 400 Hz. This presents an important consideration when designing a methodology to assess synchronization with a frequency modulated auditory stimulus.

The data discussed above points towards discrepancies between the saliency of auditory stimuli when compared to visual stimuli, as visual stimuli appear to have more than one salient point. For VC, given the lack of difference between the right and left anchoring values as shown with $AI_{spatial}$ it appears that the participants could discriminate between the two endpoint colours however further research investigating the salient points of this stimulus is required. As for the VP condition the saliency at the two endpoints has been discussed previously (see Hajnal et al. 2009). This discrepancy between the salient points of the two modalities (visual and auditory) when they are panned could partially account for the observed differences in synchronization stability. One possible method of overcoming this bias would be to ask participants to synchronize both their left and right endpoints of movement with the high frequency, e.g. 800 Hz. This could be achieved by doubling the modulation frequency so that a single oscillation would be classified as a peak-to-peak modulation between each 800 Hz.

Evidence of better sensorimotor synchronization with bimodal compared to unimodal stimuli was demonstrated with the CRP and SD CRP results, supporting previous research (Kelso et al. 2001; Wing et al. 2010; Elliott et al. 2010; Zelic et al. 2012; Varlet et al. 2012) however at a condition level, there is only limited evidence of any benefit relating to multisensory integration. The maximum likelihood estimation model discussed in Ernst & Bülthoff (2004) emphasises that relevant information from different modalities is optimally integrated. Specifically, this integration was only evidenced in the AC-VC condition, which was significantly more stable than both of its unisensory counterparts, AC and VC. Individually, AC and VC were the two unisensory conditions with the highest variability within their own modalities. Given this high variability, when these stimuli were presented together (AC-VC) it could be assumed that this was the bimodal condition with the largest task difficulty. With the task difficulty increased compared to the other bimodal conditions this may have placed a higher demand on the perceptual system to integrate the sensory information optimally, resulting in the bimodal benefit observed with this condition. However, further research investigating the effect that task difficulty has on multisensory integration is needed. Additionally, the lack of any significant differences between the three other multisensory stimuli and their unisensory counterparts could be an indication that the perceptual system did not require the integration of the two modalities and instead relied on the visual stimulus. This is evidenced by the fact that these bimodal conditions have very similar levels of CRP and SD CRP as their unisensory visual counterparts.

The discrepancy between the bimodal findings from this study and that of other multisensory studies may be related to the structure or patterning of information in the stimuli. In a majority of the multisensory studies that found a bimodal benefit, i.e. synchronization was significantly improved with bimodal compared to unimodal conditions, the stimuli had a discrete structure. This discrete structure was coupled with a synchronization task that was also discrete. While Varlet et al. (2012) used both discrete and continuous stimuli their task specified only one discrete point in the movement. Thus, the discrete structure of the information meant that participants were aiming to synchronize with only one point during each oscillation and were not required to maintain synchronization continuously during the whole oscillation. In contrast with this the current study provided a different structure of information that was presented to the participants. The stimuli in this study all had a continuous structure and were required to synchronize their movements with the entire stimulus not one discrete point. These key differences in terms of both the structure of the stimuli and the synchronization task may have led to the observed differences between this study and other work in this area. More specifically, the organisation of timing a continuous movement with continuous information is known to be a different process compared to the timing of discrete movements with discrete information (Torre and Balasubramaniam 2009).

The supplementation of spatial information for a visual stimulus appeared to be key for stabilising synchronization in both the unimodal visual and the bimodal conditions. This was indicated by a significant reduction in SD CRP for the bimodal conditions containing VP (AC-VP and AP-VP) compared to those containing VC (AC-VC and AP-VC). The poor spatial saliency of the auditory stimulus and the low levels of CRP and SD CRP already observed with VP may have affected the integration of the stimuli and led to this visual bias in the bimodal conditions resulting in a lack of significant differences between the best unimodal condition (VP) and the two best bimodal conditions (AC-VP and AP-VP). Future research may look to combine the different spatio-temporal strengths of visual and auditory stimuli using a spatially orientated oscillating visual stimulus and temporally orientated discrete beep in an attempt to maximise the multisensory integration potential for synchronization. Alternatively, a more difficult task may help exacerbate the optimal integration of the senses as previously mentioned.

The temporal anchoring results indicated that the bias towards the high pitch observed with AP in the unimodal conditions disappeared in the bimodal conditions containing the same auditory stimulus. The lack of any temporal bias towards the high frequency of AP in the bimodal conditions containing this stimulus could be an indication of sensory integration however it is more likely that participants were biased towards the visual stimulus, as discussed above. Further research assessing the specific weighting of these sensory modalities in a multisensory environment is required in order to fully determine whether integration or sensory bias is taking place.

The MLE model of multisensory integration attempts to explain how the brain optimally weights different sensory information, in terms of it's reliability, in order to develop a robust percept of a given multisensory environment (Ernst and Bülthoff 2004). Based on this concept it could be assumed that for a multisensory stimulus if the two modalities are spatially and temporally aligned then the information will be optimally integrated to produce more stable synchronization when compared to synchronization with their unisensory counterparts. Elliott et al. (2010) used the MLE model to assess synchronization with bimodal stimuli in different conditions using tactile, auditory and visual stimuli with one of the two modalities containing ‘jitter’, which was added to reduce the reliability of the modality and see if the expected weighting shift would occur in the direction of the other modality. Their results indicted that the MLE model in general accounted for the weighting across their different conditions, except at high levels of jitter. Using this approach for the stimuli used in the current study would be extremely useful for understanding the weighting of the sensory integration.

In general the findings from this study fit in well with the Gibsonian perspective of perception-action. From Gibson’s perspective the information picked up from a stimulus must be meaningful and specific in relation to the task that is being performed (Gibson 1986). The differences between the two modalities in the unimodal conditions clearly shows that the information provided in the auditory modality was not as meaningful for the task as the visual modality. The specific information contained within the auditory modality may not have been very salient as clearly shown with the differences in anchoring between the left and right endpoints. Thus, this issue of saliency interfered with the perception of task-relevant information with this modality and resulted in the observed differences between the auditory and visual stimuli. The lack of differences between the temporal and spatio-temporal auditory stimuli may seem to go against Gibson’s perspective since the addition of spatial information should provide more meaningful and specific information that is clearly relevant and congruent with the task. However, these results again emphasise the importance of saliency with perceiving information from the environment. In this case the saliency issues with the endpoints, 800 Hz and 400 Hz, may have disrupted the perception of this task-relevant spatial information. Thus, the information provided in the spatio-temporal condition was not extremely meaningful for the given task since it could not be accurately perceived.

The lack of any significant improvement in synchronization performance with the bimodal compared to unimodal stimuli can also be explained through Gibson’s perspective of perception-action. In order for the bimodal stimuli to improve synchronization compared to the unimodal stimuli additional information would need to be available for participants that is meaningful and specifically related to the task. Essentially more information relating to the task was provided in the bimodal conditions since participants perceived information from two modalities, which may be interpreted as the reason for expecting an improvement in these bimodal conditions. However, part of the extra information in the bimodal conditions was in the form of the auditory stimuli which due to saliency issues discussed above did not provide any additional information that was not already provided by the visual modality. Thus, the saliency of the visual modality combined with the lack of saliency in the auditory modality resulted in the lack of any differences between the bimodal and unimodal conditions.

4.6 Conclusion

The results from this current article represent an important step towards understanding how we synchronize with and integrate audio-visual continuous stimuli. At the unimodal level, the results indicated that synchronization was better with visual compared to auditory stimuli. Importantly, it was shown that the benefit associated with supplementing a temporal stimulus with spatial information was only present for visual stimuli, which may relate to the different saliencies between visual and auditory stimuli in the spatial and temporal domains. Overall, the results provided evidence of optimal integration in the bimodal conditions as they produced significantly better synchronization levels compared to the unimodal conditions however when the data was analysed across the individual conditions there was only limited evidence of optimal integration. This evidence lay with the AC-VC condition, which had significantly improved synchronization stability, compared to its unisensory counterparts. While these results reveal a lot about multisensory synchronization and allude to some possible mechanism of multisensory integration, further studies should aim at assessing the weighting of different sensory modalities in a synchronization task and the role that task difficulty may play in sensory integration.

4.7 Funding source

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4.9 Link between Chapter 4 and Chapter 5

Purpose of Chapter 4:

The purpose of Chapter 4 was twofold. Firstly, the unimodal conditions compared the role of spatial information when synchronizing with auditory or visual stimuli. While the results from the visual stimuli supported the findings from Chapter 3, it appeared that the supplementation of spatial information had no influence on synchronization with an auditory stimulus. The issue of saliency was raised with this modality since a bias towards one particular endpoint was observed potentially explaining the lack of results relating to spatial information. Secondly, the main results relating to the bimodal stimuli unexpectedly indicated that there was only limited improvement in synchronization with these conditions compared to their unisensory counterparts. The high saliency of the visual stimulus in these bimodal conditions coupled with the low task difficulty may have contributed to these results.

Purpose of Chapter 5:

Based on the results from Chapter 4, two main objectives emerged. Firstly, the results indicated that the supplementation of spatial information did not improve synchronization with the auditory modality implying that the perception of relative direction may be important for audition. Thus, Experiment 1 aimed to specifically explore the role of relative direction with this modality while also comparing it with vision. In this experiment, the participants were asked to synchronize with auditory or visual stimuli presented in unimodal conditions. For all of the conditions, these stimuli were occluded in different locations and by different amounts. The second objective was to assess how sensory integration is influenced by occlusion, essentially looking at the ability of one modality to “fill-in” for occlusion in another modality. In this experiment participants synchronized with audio-visual stimuli where one or both modalities were occluded.

Chapter 5: The Effect of Occlusion on Synchronizing with Auditory and Visual Stimuli

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5.1 Abstract

Bingham (2004) proposed that the perception of relative direction is the important task-relevant information required in visuomotor coordination. Research has shown support for this claim using visual stimuli (Hajnal et al. 2009) but little is known about the perception of relative direction with an auditory stimulus. Thus, the first experiment in this paper addressed whether the perception of relative direction with an auditory stimulus plays an important role in stabilising coordination. Participants swung a wrist pendulum in synchronization with auditory and visual stimuli presented in unimodal conditions with different amounts and locations of occlusion. The results supported the previous findings relating to the visual stimulus and showed that the perception of relative direction at the endpoints of an auditory stimulus plays an even more essential role for this modality. The second experiment aimed at assessing how occlusion in one modality could be "filled-in" by another modality. In the same task as experiment 1, audio-visual bimodal stimuli were presented where either one or both modalities were occluded in different locations and by different amounts. The results indicated that the presence of a non-occluded modality significantly improved coordination and that the "filling-in" effect may have occurred. Importantly, there was also some evidence suggesting that this sensory integration was mediated by the task difficulty.

***Key words**: multisensory; integration; occlusion; relative direction; task difficulty;*

5.2 Introduction

Sensorimotor synchronization, the ability to coordinate rhythmic movement with an external stimulus (Repp and Su 2013), is an ubiquitous aspect of human behaviour from social interaction to skilled performance (Wing et al. 2010). The dynamics of this interaction between a person and the environment is shaped by both informational and neuromuscular constraints. The former relates to the perception of different features of the environment such as visual and auditory information while the latter is related to physical properties of the movement itself. In order to understand how the dynamics of a movement system are affected by these constraints specific experimental strategies can be employed whereby these informational (and neuromuscular) constraints are manipulated and the resulting movement patterns examined (Williams et al. 1999). For example, Roerdink et al. (2013) manipluated neuromuscular constraints in a wrist cycling task by changing participants' wrist posture. Their results indicated that these constraints had a significant impact on synchronization where the wrist posture position mediated anchoring in the same location (i.e. flexed wrist posture resulted in anchoring at peak flexion). Not withstanding the importance of these neuromuscular constraints many researchers have focused on the perceptual (informational) constraints affecting motor coordination.

The dynamical systems theory supports this informational basis for motor coordination as it describes the coupling between systems, for example a person and the environment, as informational (Kelso 1995). Research investigating interpersonal coordination has helped to shed some light on these informational constraints that affect motor coordination. For example, Schmidt et al. (2007) have demonstrated that the presence of an environmental stimulus can entrain a participant's movement even when the goal is to move at a different frequency to the stimulus. This entrainment can be affected by the ability to perceive the relevant information from the environment and it has been shown that attending to the stimulus is an important factor for strengthening the unintentional coupling between movement and an external rhythm (Schmidt et al. 2007; Richardson et al. 2007). Also it has been shown that this coupling is weakened as the difference in the individual oscillation frequencies increases (Lopresti-Goodman et al. 2008). While this research highlights the importance of information in coupling movement and environmental stimuli, a key question for sensorimotor synchronization remains unanswered and relates to what information is used to control action.

Bingham and colleagues hypothesized that the perception of relative direction of a given stimuli may be the information used in the control of action (Bingham et al. 1999; Zaal et al. 2000; Bingham et al. 2001). In these studies participants were required to make judgments based on the relative phase and phase variability between two horizontally oscillating visual stimuli. Their findings indicated that the general patterns of stability found in synchronization studies were replicated in the perception of relative phase and its variability. More precisely judgments were most reliable at 0° followed by 180° while all other phases outside of these two were very unstable and as frequency increased phase was judged with more variability for 180° but not 0°. These results may be transferable to coordination studies and the ability to perceive relative phase may be an important factor in synchronization (Bingham et al., 1999). These findings were formalised in the Perceptually Driven Dynamical model developed by Bingham (2004). This model proposed relative direction of movement as the important information required for synchronization, which depends on relative speed in order for it to be detected. Subsequent studies have provided evidence that strongly supports relative direction as the information that is used for stabilizing coordination in rhythmic synchronization tasks (Wilson et al. 2005; Wilson and Bingham 2008; Snapp-Childs et al. 2011).

One particular study by Hajnal et al. (2009) addressed the importance of perceiving relative direction in a synchronization task by reducing the availability of this information. Participants had to synchronize wrist pendulum movements with a horizontally oscillating visual stimulus that was occluded in different locations and by different amounts. Their hypothesis was that when relative direction is occluded at the endpoints variability in movement would significantly increase[3]. Their results supported this hypothesis indicating significant increases in the variability of relative phase when the endpoints compared to other locations were occluded while the amount of occlusion did not have a significant impact on synchronization. These results provide further support for Bingham's Perceptually Driven Dynamical model of coordination. As highlighted by the authors, coordination was still possible when the endpoints were occluded suggesting that information contained between the endpoints is also important for coordination. Experiment 1 in this current paper will aim to expand on this work by Hajnal and colleagues by using the same paradigm to investigate the importance perceiving relative direction with two different sensory modalities: a visual and an auditory stimulus.

While Bingham's model relates only to visual coordination, it is possible that the perception of relative direction for an auditory stimulus is important as well. Differences arise between visual and auditory stimuli since spatial perception is better for the former than the latter modality (Welch and Warren 1980). Thus, relative direction may be more difficult to detect with the auditory modality. Based on this assumption the perception of relative direction when it is most salient, i.e. at the endpoints when relative speed is slow, may be even more important for synchronization with auditory compared to visual stimuli. However, research suggests that while the endpoints of an auditory stimulus may be important, information between these endpoints can also help to provide necessary information to help stabilise coordination. Recent research by Rodger & Craig (2011) assessed synchronization with both discrete and continuous auditory stimuli, both of which contained spatial information. Their results indicated that information between the two discrete endpoints of the stimulus helped to stabilise coordination in the continuous conditions. These results are similar to previous work using visual stimuli that indicate the importance of information between two discrete points (Buekers et al. 2000). Given the poor spatial perception of the auditory modality it is possible that

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[3] The end points are considered as the most salient points since relative speed slows down at these locations allowing for relative direction to be easily perceived.

occlusion of relative direction in locations other than the endpoints could also negatively impact the synchronization.

The aim of this first experiment is to replicate and expand upon the work by Hajnal et al. (2009). Participants will be asked to perform a synchronization task with a visual and auditory stimulus that will be occluded by different amounts and in different locations. It is hypothesised that the findings relating to the visual stimulus will support those found by Hajnal et al. (2009). Regarding the auditory stimulus, based on the discussion in the above paragraph it seems plausible that the endpoints of an auditory stimulus are a particularly salient point in the stimulus that may be important for synchronization. Thus, it is hypothesised that the occlusion of these points, i.e. the endpoints, will have a significant negative effect on synchronization performance compared to the other occlusion locations. Based on the findings from Hajnal et al. (2009) and the known strength of vision compared to audition in the spatial domain it is hypothesised that overall synchronization performance will be significantly better with the visual compared to auditory conditions.

5.3 Experiment 1

5.3.1 Methodology

5.3.1.1 Participants

Twelve volunteers (six females and six males) between the age of 18 and 33 years (21.50 yrs. ±5.20) took part in the experiment. All participants were right handed, had normal or corrected to normal vision and no known history of neuromuscular deficits that would affect their participation. Colour blindness was assessed using a series of Ishihara pictures and none of the participants had any form of colour blindness. No compensation was given to the participants for their involvement in the experiment. Ethical approval was received from the Dublin City University Research Ethics Committee (DCUREC/2011/038).

5.3.1.2 Stimuli

Two different modalities were used in the experiment, a visual stimulus and an auditory stimulus. A screen (Dell Trinitron Ultrascan 1600HS Series CRT Monitor, Model D1626HT) displayed the visual stimulus and was placed at eye level approximately 1 m from the participants. The visual stimulus appeared as a square (6 × 6 cm) oscillating horizontally across the screen in a sinusoidal fashion at 0.75 Hz with an amplitude of 42.5 cm and also oscillated sinusodially at the same frequency between a red (left endpoint) and yellow (right endpoint) colour. The visual stimulus was occluded at three different locations, End (0°/180°), Middle (90°/275°) and FortyFive (45°/135°/225°/315°) and by three different amounts (80°, 120° and 160°) creating a total of nine visual conditions. The occlusion was created by displaying a grey rectangle at the specific location and by the specific amount. The auditory stimulus was presented through noise cancelling headphones and consisted of a continuous tone that modulated from a low pitch (400 Hz) to a high pitch (800 Hz) in a sinusoidal fashion at 0.75 Hz. This frequency-modulated tone also contained a spatial component that panned the sound between left and right ear. The high pitch was most salient when the tone had panned all the way to the left and the low pitch was most salient when the tone had panned all the way to the right. This stimulus was occluded using the same locations and amounts by applying a fade out/in to the auditory signal creating a total of nine auditory conditions.

Importantly, it must be noted that the aim of this type of occlusion used was to occlude a specific amount of the overall trajectory (in degrees) of the stimuli. As a consequence of this aim the amount of time that the stimulus was occluded for slightly differed with each of the occlusion locations. Due to the sinusoidal trajectory used the stimuli slowed down at the endpoints and this meant that the total time of occlusion was slightly larger for the End compared to Middle and FortyFive occlusion locations. While this difference in total time of occlusion was very small it is still a limitation of the methodology that must be stated and may have had an impact on the overall results.

The visual stimulus was created in Matlab using the Psychophysics Toolbox extensions (Pelli 1997; Brainard 1997; Kleiner et al. 2007) while the auditory stimulus was created using Supercollider (McCartney 2002). Data was recorded at 100 Hz using a Measurement Computing Data Acquisition Device (Measurement Computing, USB-1608FS) and stored for further analysis. Data collection and stimulus presentation were controlled in Matlab using the Psychophysics Toolbox extensions.

5.3.1.3 Procedure

Upon arrival participants were handed an information sheet about the experiment and were asked to sign an informed consent form. Following this, the experiment was explained in two parts, 1) familiarisation and 2) experimentation. Participants sat in a height adjustable chair with a forearm support and gripped an aluminium pendulum with their right hand. The pendulum was 49 cm long with a weight of 53 g attached at the end. Its eigenfrequency was 0.75 Hz. Participants were prevented from viewing the pendulum's movements with a wooden cover and the arm of the participant was also concealed using a sliding panel. Participants swung the pendulum in a darkened room, through the frontal plane by pronating and supinating their forearm and were told to move the pendulum with an amplitude of 45 degrees to the right and 45 degrees to the left from the resting position of the pendulum. An example of the experimental setup is shown in Figure 1.

During the familiarisation stage, participants practiced synchronizing the movements of the handheld pendulum with the non-occluded visual and auditory stimuli. Each of the stimuli were presented three times at a frequency of 0.75 Hz. Additional practices were provided if required by the experimenter in order to ensure an understanding of the different experimental conditions. For the visual condition, participants had to swing to the left as the square moved left fading towards red and to the right as the square moved right fading towards yellow, synchronizing the endpoint of the movements with the square's endpoints. For the auditory condition, participants were required to swing the pendulum to the left as the sound panned to the left ear fading towards a high pitch and to the right as the sound panned to the right ear fading towards a low pitch, synchronizing the endpoint of the movements with the sound's endpoints. Following the familiarisation participants were told that during the main experiment the same stimuli would be presented and the task would remain the same but that the stimuli would be occluded by different amounts and in different locations. Importantly, it was highlighted that the task was still to synchronize the movements of the pendulum with the stimulus, even though parts of it will be occluded.

The design of the experiment was a 2 (Modality) × 3 (Occlusion Location) × 3 (Occlusion Amount), resulting in a total of 18 conditions. Participants completed one trial of each of the 18 randomised conditions for each of the two blocks. There was a 30 sec break after each 40 sec trial and a five minute break between blocks.

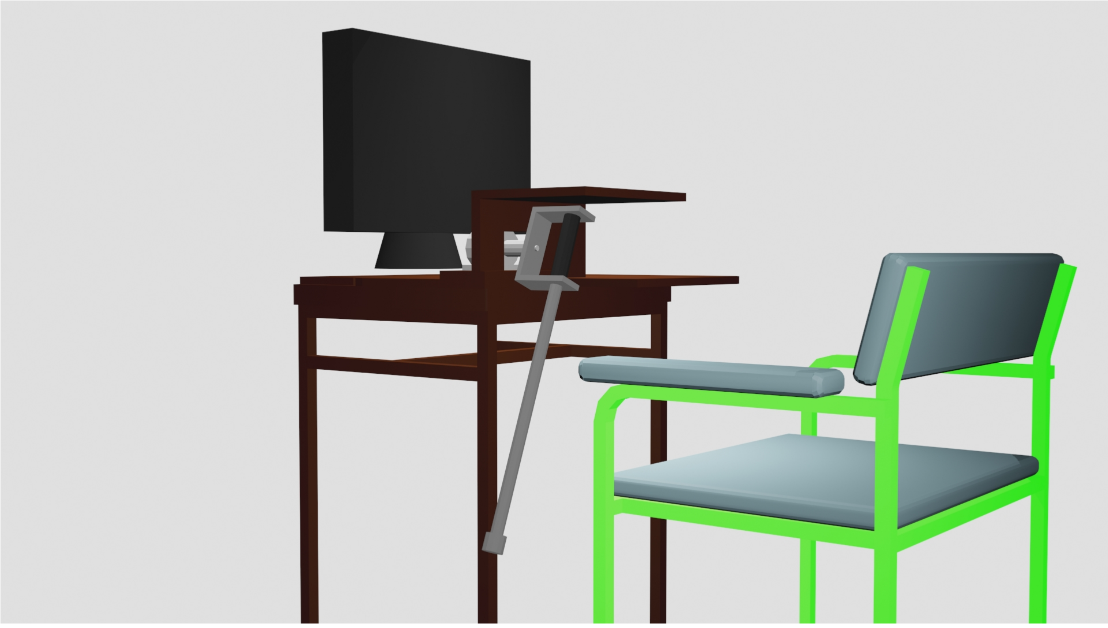

Figure 1 Example of experimental setup

5.3.1.4 Data reduction

Before any analysis the first 10 seconds of data were removed and the remaining 30 seconds were low pass filtered using a 10 Hz Butterworth filter. Data were then normalised between ±1 using min max scaling. All data were averaged across each of the two trials for the 18 experimental conditions. In order to assess the degree of coordination between the participants and the stimulus, the Continuous Relative Phase (CRP) was used. CRP was calculated using a Hilbert Transform and scaled between 0° and 180°. The first and last cycles of each trial were removed due to distortions caused by the Hilbert Transform during the computation of relative phase (Pikovsky et al. 2003). Based on these CRP values the Standard Deviation (SD) of CRP was calculated, which allowed for an assessment of the stability of coordination. In order to determine the lead/lag nature of the participant's movement in relation to the stimulus, the average CRP at the endpoints of the stimulus was calculated using a range of ±180˚, negative values indicate participants leading the stimulus while positive values indicate participants lagging the stimulus.

In order to examine any reductions in spatial or temporal variability at the endpoints of the movement, anchoring was calculated. Spatial anchoring was calculated using the SD of the participant's movement at the endpoints of their pendulum swing (SD in degrees). Temporal anchoring constituted the variability in the asynchrony between the stimulus arrival time at an endpoint and the corresponding time of the participant's arrival (SD in ms). A low value for either of these anchoring variables indicates a reduction in the variability at the endpoint of the movement. The anchoring data were divided into two categories, right and left endpoint of the movement. The Spatial and Temporal Anchoring Index, $\mathrm{AI}_{\mathrm{spatial}}$ and $\mathrm{AI}_{\mathrm{temporal}}$ respectively, were then calculated using the following equation (Roerdink et al. 2008):

$$\mathrm{AI} = \frac{\mathrm{SD}_l}{\mathrm{SD}_l + \mathrm{SD}_r},$$

where SD_l and SD_r represent the spatial or temporal anchoring at the left and right endpoints respectively. An anchoring index of 0.5 indicates that the anchoring is the same on the left and right. A value less than 0.5 indicates more anchoring on the left than the right and a value greater than 0.5 indicates more anchoring on the right than the left.

5.3.1.5 Statistical analysis

All the statistical analysis was performed with SPSS (IBM SPSS Statistics 20) using the averaged data across the two trials and the twelve participants. A 2 (Modality) × 3 (Occlusion Location) × 3 (Occlusion Amount) repeated-measures analysis of variance (ANOVA) was used to assess CRP, SD CRP, Left endpoint Anchoring, Right endpoint Anchoring, $\mathrm{AI}_{\mathrm{spatial}}$ and $\mathrm{AI}_{\mathrm{temporal}}$. Sphericity was assessed for each of these variables and the Greenhouse and Geisser's correction for the degrees of freedom was applied when sphericity was not met. Post Hoc analysis using Bonferroni's correction was used where necessary in order to detail the direction of significant effects. One-sample *t*-tests were used to assess the differences from zero of the average CRP (scaled to ±180°). Additionally, $\mathrm{AI}_{\mathrm{spatial}}$, and $\mathrm{AI}_{\mathrm{temporal}}$ were also assessed using one-sample *t*-tests to see whether the anchoring index differed significantly from 0.5, which would indicate more anchoring at one of the two endpoints. All of the *t*-tests were performed on Occlusion Amount and Occlusion Location for each of the modalities. The size of the effect for all of the ANOVA analysis was reported by means of the partial eta squared (η^2_p).

5.3.2 Results

5.3.2.1 Mean Continuous Relative Phase

The 2 (Modality) × 3 (Occlusion Location) × 3 (Occlusion Amount) repeated-measures ANOVA on CRP yielded a significant main effect for Modality ($F_{1, 11}$ = 91.82, p < .01, η^2_p = .89), revealing higher CRP values, indicating lower synchronization performance, with the Auditory (34.0°) compared to Visual (10.1°) conditions (Fig. 2). There was also a significant main effect for Occlusion Location ($F_{1.33, 14.57}$ = 11.68, p < .01, η^2_p = .52), which showed higher CRP values with End (32.6°) compared to Middle (16.6°) and FortyFive (17.0°) Occlusion. Occlusion Amount was not found to be significant ($F_{2, 22}$ = 3.05, p > .05, η^2_p = .22). The interaction between Modality and Occlusion Location was also found to be significant ($F_{1.32,14.54}$ = 6.81, p < .05, η^2_p = .38). A simple effects analysis revealed higher CRP values for Auditory compared to Visual conditions across all Occlusion Locations. The analysis of this interaction also revealed higher CRP values for End compared to Middle and FortyFive Occlusion for both modalities. None of the other interactions were found to be significant; Modality and Occlusion Amount ($F_{2,22}$ = 0.13, p > .05, η^2_p = .01), Occlusion Amount and Occlusion Location ($F_{4,44}$ = 2.47, p > .05, η^2_p = .18), Modality, Occlusion Amount and Occlusion Location ($F_{4, 44}$ = 1.65, p > .05, η^2_p = .13).

One-sample *t*-tests revealed significant results for both Occlusion Amount and Occlusion Location. When the end was occluded participants displayed CRP values significantly different for zero but only with the auditory modality. Similarly, conditions with 80° and 120° occlusion were significantly different from zero but only for the auditory modality. All of these CRP values were negative indicating that participants tended to lead the stimulus in these conditions. A positive mean value was only found when FortyFive occlusion was present with the auditory modality (A_o), indicating the participants tended to follow the stimulus in this condition although this was not significantly different from zero. Table 1 displays the results from the one-sample *t*-tests for CRP.

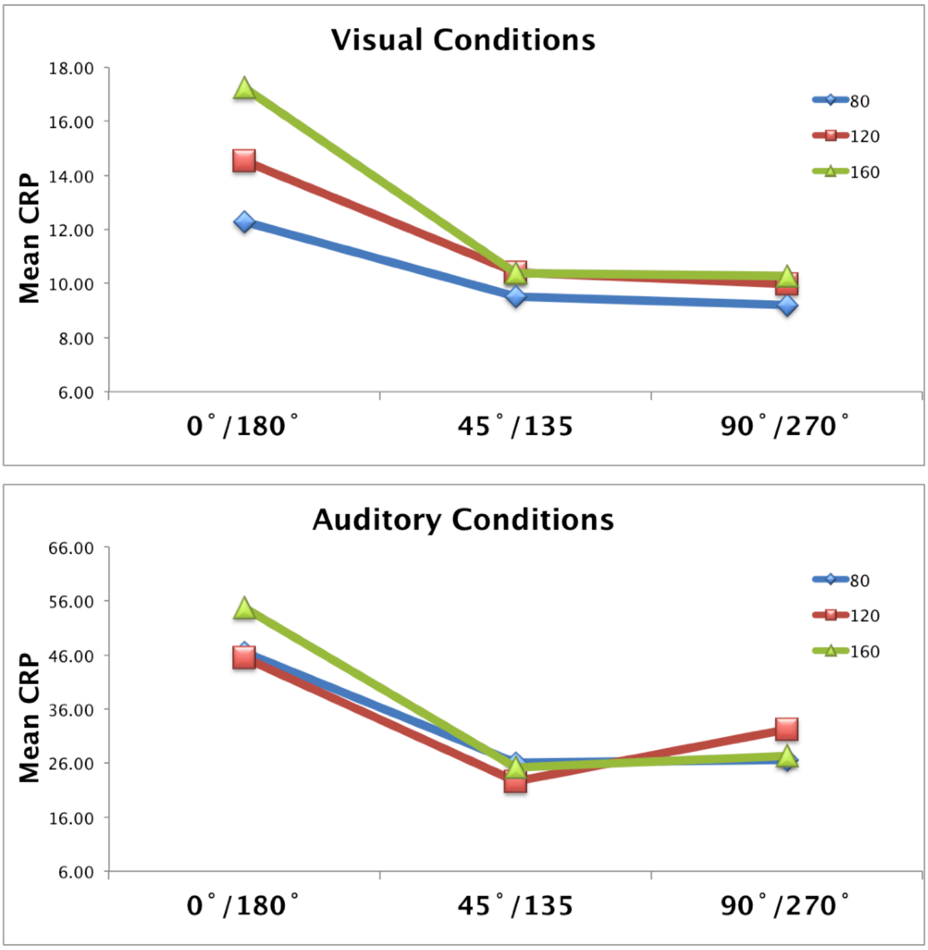

Figure 2 Mean Continuous Relative Phase for all conditions

Categories	Mean	SD	t	df	Sig (2-tailed)
V_o End	-4.27	9.99	1.48	11	.167
V_o Fortyfive	-0.13	5.93	.08	11	.941
V_o Middle	-0.97	5.74	.58	11	.571
A_o End	-44.13	28.10	5.44	11	.000
A_o Fortyfive	6.02	23.48	-.89	11	.393
A_o Middle	-6.12	21.20	1.00	11	.339
V_o 80	-1.41	6.91	.71	11	.493
V_o 120	-0.75	7.22	.36	11	.727
V_o 160	-3.21	6.60	1.68	11	.121
A_o 80	-16.56	20.50	2.80	11	.017
A_o 120	-14.41	22.23	2.25	11	.046
A_o 160	-13.26	23.33	1.97	11	.075

Table 1 CRP one-sample *t*-tests

5.3.2.2 Standard Deviation of Continuous Relative Phase

The 2 (Modality) × 3 (Occlusion Location) × 3 (Occlusion Amount) repeated-measures ANOVA on SD CRP yielded a significant main effect for Modality ($F_{1,11} = 81.53$, $p < .01$, $\eta^2_p = .88$), revealing higher SD CRP values, indicating lower synchronization performance, with the Auditory (10.2°) compared to Visual (6.2°) conditions (Fig. 3). There was a significant main effect for Occlusion Location ($F_{2,22} = 17.78$, $p < .01$, $\eta^2_p = .62$), which showed higher SD CRP values with End (9.7°) compared to Middle (7.1°) and FortyFive (7.9°) Occlusion. The interaction between Modality and Occlusion Amount was also found to be significant ($F_{2,22} = 4.64$, $p < .05$, $\eta^2_p = .30$). A simple effects analysis revealed that with the visual modality 80° occlusion (5.8°) had significantly lower SD CRP compared to 160° occlusion (6.6°). This analysis also revealed that Auditory conditions had a significantly higher SD CRP compared to Visual conditions for all Occlusion Amounts. None of the other interactions were significant; Modality and Occlusion Location ($F_{2,22} = 2.07$, $p > .05$, $\eta^2_p = .16$), Occlusion Amount and Occlusion Location ($F_{4,44} = 0.87$, $p > .05$, $\eta^2_p = .07$), Modality, Occlusion Amount and Occlusion Location ($F_{4,44} = 0.98$, $p > .05$, $\eta^2_p = .08$).

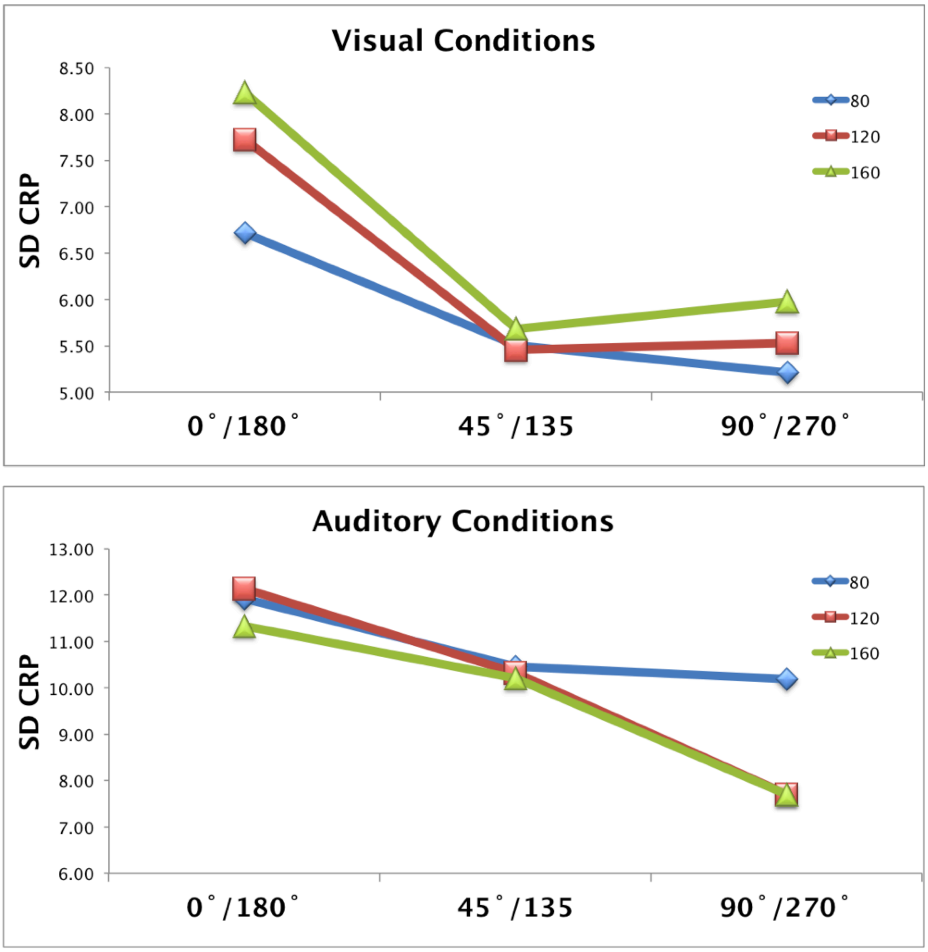

Figure 3 Standard Deviation of Continuous Relative Phase for all Conditions

5.3.2.3 Spatial Anchoring

Since there were two anchoring points in the rhythmic movement separate ANOVA's were performed on both Left and Right in order to establish any changes in spatial anchoring at these individual points. The 2 (Modality) × 3 (Occlusion Location) × 3 (Occlusion Amount) repeated-measures ANOVA's performed on Left Spatial Anchoring revealed no significant results; Modality ($F_{1, 11} = 1.05$, $p > .05$, $\eta^2_p = .09$), Occlusion Amount ($F_{2, 22} = 0.03$, $p > .05$, $\eta^2_p = .00$), Occlusion Location ($F_{2, 22} = 0.74$, $p > .05$, $\eta^2_p = .06$), Modality and Occlusion Amount interaction ($F_{2, 22} = 1.74$, $p > .05$, $\eta^2_p = .14$), Modality and Occlusion Location ($F_{2, 22} = 1.25$, $p > .05$, $\eta^2_p = .10$), Occlusion Amount and Occlusion Location interaction ($F_{4, 44} = 1.15$, $p > .05$, $\eta^2_p =$

.09), Modality, Occlusion Amount and Occlusion Location interaction ($F_{4,44} = 0.44$, $p > .05$, $\eta^2_p = .04$). The 2 (Modality) × 3 (Occlusion Location) × 3 (Occlusion Amount) repeated-measures ANOVA's performed on Right Spatial Anchoring also revealed no significant results; Modality ($F_{1,11} = 1.04$, $p > .05$, $\eta^2_p = .09$), Occlusion Amount ($F_{2,22} = 0.08$, $p > .05$, $\eta^2_p = .01$), Occlusion Location ($F_{2,22} = 0.37$, $p > .05$, $\eta^2_p = .03$), Modality and Occlusion Amount interaction ($F_{2,22} = 3.06$, $p > .05$, $\eta^2_p = .22$), Modality and Occlusion Location interaction ($F_{2,22} = 0.39$, $p > .05$, $\eta^2_p = .03$), Occlusion Amount and Occlusion Location interaction ($F_{4,44} = 1.29$, $p > .05$, $\eta^2_p = .11$), Modality, Occlusion Amount and Occlusion Location interaction ($F_{4,44} = 0.22$, $p > .05$, $\eta^2_p = .02$).

This indicates that the modifications made to both modalities in terms of Occlusion Location and Occlusion Amount had no significant impact on the spatial structure of the participant's movement, namely the ability to anchor movement at the reversal points. The Spatial Anchoring values displayed in Fig. 4 are averaged across left and right. The one sampled *t*-test revealed that when FortyFive occlusion was present with the visual modality $AI_{Spatial}$ was significantly different from 0.5 indicating more anchoring on the left than the right endpoint. No other conditions were found to be significantly different from 0.5. The full results for $AI_{Spatial}$ are presented in Fig. 5. Table 2 displays the results from the one-sample *t*-tests for $AI_{Spatial}$.

Categories	Mean	SD	t	df	Sig (2-tailed)
V_o End	.49	.04	-.55	11	.597
V_o Fortyfive	.48	.02	-3.11	11	.010
V_o Middle	.48	.04	-1.58	11	.142
A_o End	.49	.04	-1.14	11	.279
A_o Fortyfive	.48	.04	-1.61	11	.136
A_o Middle	.49	.04	-1.27	11	.231
V_o 80	.49	.05	-.94	11	.369
V_o 120	.49	.04	-1.08	11	.303
V_o 160	.48	.04	-1.85	11	.092
A_o 80	.48	.05	-1.64	11	.130
A_o 120	.49	.04	-1.02	11	.331
A_o 160	.49	.05	-1.08	11	.305

Table 2 $AI_{Spatial}$ one-sample *t*-tests

5.3.2.4 Temporal Anchoring

The 2 (Modality) × 3 (Occlusion Location) × 3 (Occlusion Amount) repeated-measures ANOVA on Temporal Anchoring Left yielded a significant main effect for Modality ($F_{1,11} = 25.64, p < .01, \eta^2_p = .70$), revealing more temporal anchoring with the Visual (31.5 ms) compared to Auditory (45.9 ms) conditions (Fig. 4). There was also a significant main effect for Occlusion Location ($F_{2,22} = 9.95, p < .01, \eta^2_p = .48$), which showed more temporal anchoring with Middle (34.9 ms) and FortyFive (37.4 ms) conditions compared to End (43.8 ms) Occlusion. No other significant findings or interactions were found; Occlusion Amount ($F_{2,22} = 0.09, p > .05, \eta^2_p = .01$), Modality and Occlusion Amount interaction ($F_{2,22} = 3.11, p > .05, \eta^2_p = .22$), Modality and Occlusion Location interaction ($F_{2,22} = 1.49, p > .05, \eta^2_p = .12$), Occlusion Amount and Occlusion Location interaction ($F_{2,22} = 1.27, p > .05, \eta^2_p = .10$), Modality, Occlusion Amount and Occlusion Location interaction ($F_{4,44} = 1.05, p > .05, \eta^2_p = .09$), A planned simple effects analysis of Modality x Occlusion Location revealed significantly more anchoring for the visual compared to auditory stimuli across all Occlusion Locations. This analysis also revealed that for the visual modality temporal anchoring was significantly greater for Middle and FortyFive compared to End

Occlusion. For the auditory modality, there were not significant findings. A planned simple effects analysis of Modality × Occlusion Amount revealed similar findings as the visual modality had more temporal anchoring than the auditory modality across all Occlusion Amounts. Also, it was revealed that the visual modality had significantly more temporal anchoring with 80° compared to 160° occlusion amount.

The 2 (Modality) × 3 (Occlusion Location) × 3 (Occlusion Amount) repeated-measures ANOVA on Temporal Anchoring Right yielded the same significant findings as Temporal Anchoring Left for Modality ($F_{1, 11} = 26.28, p < .01, \eta^2_p = .71$) and Occlusion Location ($F_{2, 22} = 9.90, p < .01, \eta^2_p = .47$). There was also a significant interaction found between Modality and Occlusion Amount ($F_{2, 22} = 3.94, p < .05, \eta^2_p = .26$) and the simple effects analysis revealed the same findings as the planned analysis from Temporal Anchoring Left. There were no other significant findings; Occlusion Amount ($F_{2, 22} = 0.09, p > .05, \eta^2_p = .01$), Modality and Occlusion Location interaction ($F_{2, 22} = 1.23$, $p > .05$, $\eta^2_p = .10$), Occlusion Amount and Occlusion Location interaction ($F_{2, 22} = 1.39$, $p > .05$, $\eta^2_p = .11$), Modality, Occlusion Amount and Occlusion Location interaction ($F_{4, 44} = 0.86, p > .05, \eta^2_p = .07$), A planned simple effects analysis of Modality × Occlusion Location revealed the same findings as Temporal Anchoring Left. The one-sampled *t*-test on $AI_{Temporal}$ (Fig. 5) revealed that none of the conditions were significantly different from 0.5. This indicated that the modification of Occlusion Location and Occlusion Amount created no bias in terms of temporal anchoring between the left and right endpoints. Table 3 displays the results from the one-sample *t*-tests for $AI_{Temporal}$.

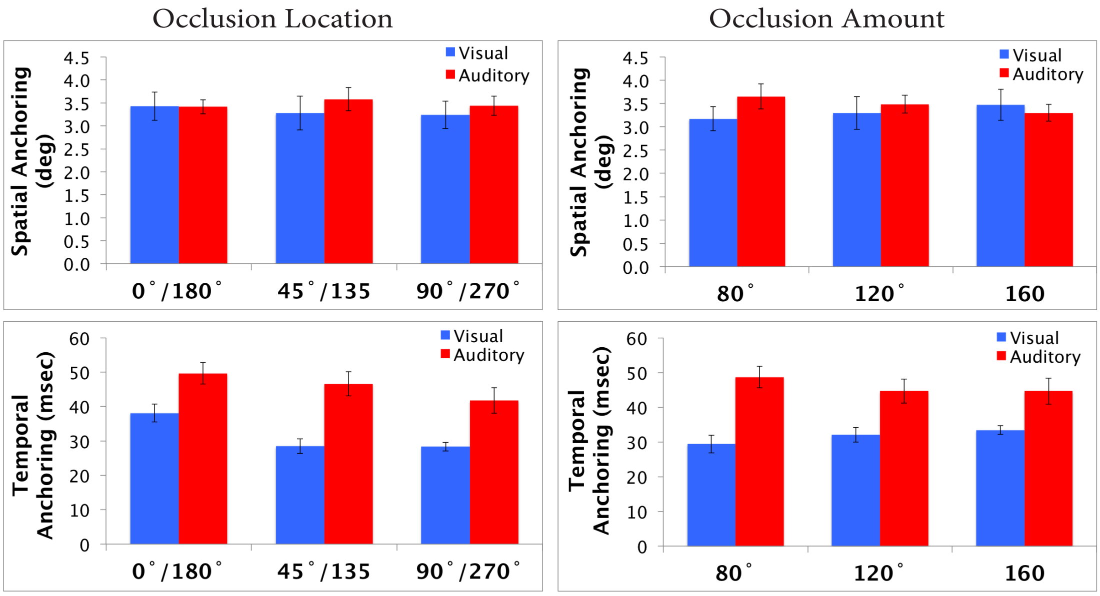

Figure 4 Mean Spatial and Temporal Anchoring values for all conditions

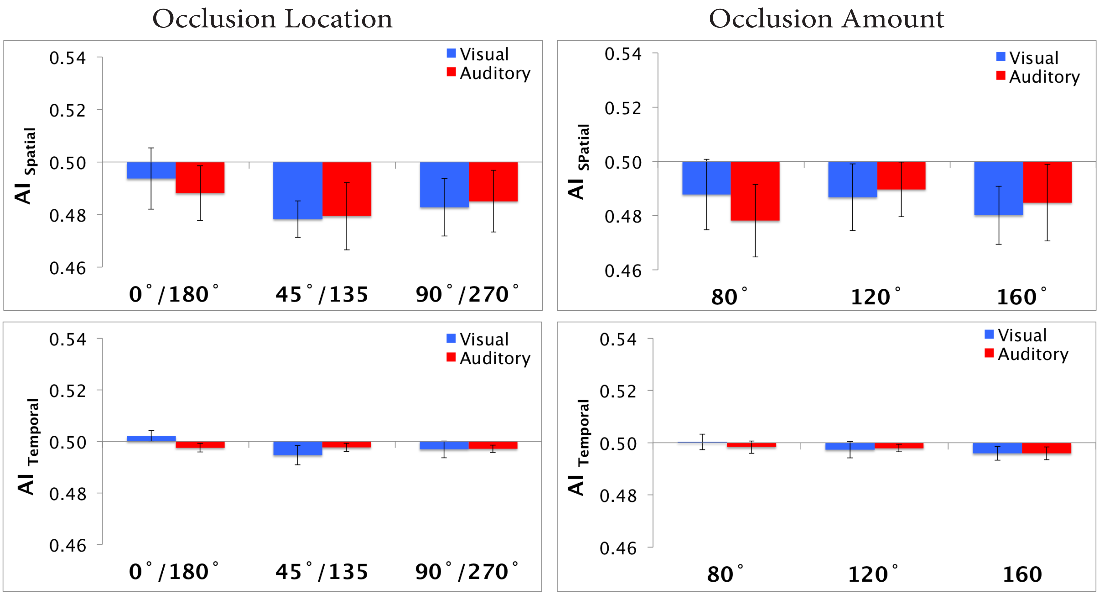

Figure 5 Mean Spatial and Temporal Anchoring index for all conditions

Categories	Mean	SD	t	df	Sig (2-tailed)
V_o End	.50	.01	.96	11	.359
V_o Fortyfive	.50	.01	-1.42	11	.184
V_o Middle	.50	.01	-.94	11	.369
A_o End	.50	.01	-1.48	11	.167
A_o Fortyfive	.50	.01	-1.48	11	.167
A_o Middle	.50	.01	-1.98	11	.074
V_o 80	.50	.01	.010	11	.925
V_o 120	.50	.01	-.83	11	.423
V_o 160	.50	.01	-1.55	11	.149
A_o 80	.50	.01	-.70	11	.497
A_o 120	.50	.01	-1.45	11	.176
A_o 160	.50	.01	-1.67	11	.123

Table 3 $AI_{Temporal}$ one-sample *t*-tests

5.3.3 Discussion

The results from experiment 1 emphasised the importance of perceiving relative direction for visuomotor coordination supporting previous work in this area (Bingham 2004; Hajnal et al. 2009). For the visual modality, when the endpoints of the stimulus were occluded, coordination was negatively affected as indicated by the increases in CRP and SD CRP compared to the two other Occlusion Locations. Temporal anchoring at both the left and right endpoints also supported these findings as more anchoring was found for Middle and FortyFive compared to End occlusion. This was expected since in the latter condition participants had no view of the synchronization endpoints as well as a lack of key information relating to the relative direction of the stimulus. However, it is important to note that the visual modality displayed resilience to the complete breakdown of coordination when the endpoints were occluded since both CRP and SD CRP were not excessively high, indicating that synchronization was still possible in these conditions. All these findings are in line with previous work by Hajnal et al. (2009) who used a similar visual stimulus and task.

Interestingly, while Hajnal and colleagues found that the amount of occlusion did not significantly impact on coordination stability several results from the current study indicated a significant effect for Occlusion Amount. While the CRP values were not affected by the amount of occlusion, the stability of the movement was affected. The synchronization was significantly more stable when only 80° of the stimulus trajectory was occluded compared to 160°. The reasons for the differences between these results and those found by Hajnal and colleagues can be attributed to differences in the patterning of information provided to participants. In the current study continuous changes to the colour of the visual stimulus were provided in addition to it's movement on screen while Hajnal et al. only provided information relating to the movement of their visual stimuli that maintained the same colour. Thus, the structure of the information provided was different since the current study provided an additional layer of information, i.e. change of colour, which could also be used during the synchronization task. The fact that participants were unable to perceive certain shades of colour during the End Occlusion may have affected their performance in the current study since the information relating to both the colour and the movement of the stimulus may have been used when synchronizing with this stimulus. Thus, adding the fading in colour to the visual stimulus may have allowed the participants to more accurately perceive changes in the amount of occlusion.

Differences in the control of the pendulum in the sagittal plane (used by Hajnal and colleagues) compared to the frontal plane (used in the current study) may have also contributed to the contrasting findings. Movements with a wrist pendulum in the sagittal plane are more restrictive than the frontal plane for participants and it is possible that because of these restrictions there is more control of movement in the frontal plane. Since the SD CRP values reported in Hajnal et al. (2009) were higher than those found in the current study for a similar visual stimulus it is possible that the movement plane influenced the contrasting results.

Additionally, it should be noted that while the size of the stimulus was similar for Hajnal and colleagues (round dot 4 cm in diameter) the amplitude of the stimulus was much larger (85 cm) and participants sat further away from the screen (1.6 m). These differences in experiment setup may have also impacted on the contrasting results for Occlusion Amount. And finally, the eigenfrequencies of the two pendulums were slightly different (0.9 Hz in Hajnal and colleagues and 0.75 in the current study). The slower motion in this experimentation implies longer duration of occlusion, which might have resulted in an increased level of task difficulty at larger Occlusion Amounts. Further research is needed in order to establish the root cause of these observed differences and may need to involve an experiment comparing these two different stimuli and the effect of movement direction on the dynamics of coordination while varying parameters such as the movement amplitude of the stimuli or the eigenfrequency of the pendulum. Additionally, it must be noted that when the stimuli were occluded at the End location this occlusion occurred for a slightly longer period of time since the sinusoidal nature of the stimulus meant that the stimuli slowed down at these endpoints and as a result this increased the occlusion time. Thus this increased occlusion time may have influenced the findings that show synchronization performance was worse when End was occluded compared to the other locations.

For the auditory modality, the information located at the endpoints of the stimulus helped to stabilise coordination, as was the case for the visual modality. This was supported with results from CRP, which indicated a lower level of coordination with End compared to both Middle and FortyFive Occlusion Locations. Importantly, while coordination was still possible with the visual modality when the endpoints were occluded, this same occlusion with the auditory stimulus resulted in a very low level of coordination. This was supported by the findings from CRP, SD CRP and temporal anchoring, where synchronization was significantly lower with the auditory compared to the visual modality across all Occlusion Locations. The timing of the movements was also affected as participants tended to precede the auditory stimulus significantly more than the visual stimulus when the endpoints were occluded, as shown from the CRP timing results. The rationale for the differences between these two modalities may relate to the saliency of these stimuli in the spatio-temporal domain. Previous research has shown that participants find spatially orientated auditory stimuli more difficult to synchronize with compared to visual stimuli (Armstrong and Issartel 2014) and may reflect the poor spatial saliency of the auditory modality (Welch and Warren 1980). Thus, due to this poor ability to perceive spatial information participants may rely more on the endpoints of the auditory modality since relative direction is more salient there. Interestingly, previous research has shown that information between the endpoints of a moving auditory stimulus might help to stabilise synchronization (Rodger and Craig 2011). However, in contrast with this the results from the current study seem to suggest that when the endpoints of the auditory stimulus were occluded the information between these points did not appear to be able to support synchronization since coordination levels were very poor.

Other key differences were also found between the auditory and visual modalities in relation to Occlusion Location. Overall, the visual modality was quite resilient to occlusion since coordination was still at a good level when the endpoints were occluded even though this was significantly worse than Middle and FortyFive Occlusion. In contrast, the auditory modality always had worse levels of coordination when compared to the visual modality and displayed different findings in terms of Occlusion Location. For SD CRP the auditory modality was only significantly better with the Middle compared to End Occlusion. The absence of significant differences between End and FortyFive Occlusion for this modality suggests that the level of difficulty was similar with both Occlusion Locations. When FortyFive Occlusion was present with the auditory modality it created an unusual intermittent sound, which may have contributed to the similarity between End and FortyFive Occlusion. Additionally, for the auditory stimulus the lack of any significant differences for temporal anchoring between conditions indicates that any disruption to the spatial information creates a similar level of difficulties regardless of the Occlusion Location. This could imply that audition is highly sensitive to the occlusion of spatial information since the perception of this type of information is poor with this modality. In general, these two sensory modalities display different levels of sensitivity to the removal of information about relative direction.

These results support the perceptual model for motor coordination proposed by (Bingham, 2004) which emphasises the importance of perceiving relative direction, specifically at the endpoints of a stimulus trajectory. The key differences noted between the visual and auditory stimuli support the Gibsonian perspective of perception and action. From this perspective the action specificity of the information provided is the most important element in relation to motor coordination. For the visual modality the results appeared to show that the information contained at the endpoints of the stimulus trajectory help to anchor the synchronization, however even when these endpoints are occluded the information picked-up between these two points provide enough task relevant information that can be used to stabilise coordination. In contrast with this the auditory modality contained information that was less salient, since it is known that synchronization is better with high compared to low frequency endpoints of a frequency modulated stimulus (Armstrong and Issartel 2014) and in general this modality is poor at detecting spatial information (Welch and Warren 1980). Thus, for this modality the endpoints reflected a vital anchoring point for synchronization and when these points were occluded the information between these two endpoints did not contain enough task-relevant information to help stabilise the motor coordination.

Overall the results from experiment 1 indicate that key information, namely the detection of relative direction, contained at the endpoints of a spatially orientated stimulus is essential for synchronization with both visual and auditory modalities. The study represents a novel investigation into the specific information that is used to stabilise synchronization with an auditory stimulus. Importantly, while the visual modality displayed resilience to occlusion at the endpoints for the auditory modality this resulted in a breakdown in coordination. The results from temporal anchoring also appear to show that this modality is more sensitive to occlusion compared to the visual modality, perhaps due to the poor ability to perceive spatial information. In contrast with findings from a previous study that utilised a similar methodology and visual stimulus (Hajnal et al. 2009), results from the current study indicate that the amount of occlusion can play a role in destabilising coordination as indicated by the significant reduction of stability when occlusion was increased from 80° to 160° with the visual modality. While these results represent an important step towards understanding the specific information that is used to synchronize movements with environmental stimuli, it is also important to investigate the integration of these stimuli. Experiment 2 will aim to address this integration of sensory information when occlusion is present.

5.4 Experiment 2

Our environment is multisensory and information from different modalities is rarely available independently of each other. The ability to integrate spatially and temporally congruent information from multiple modalities can significantly improve synchronization compared to a single modality (Carson and Kelso 2004; Van Wanrooij et al. 2009; Varlet et al. 2012). Despite the benefit associated with multisensory stimuli, a previous study by Armstrong and Issartel (under review) seems to indicate that auditory and visual stimuli presented in bimodal conditions with spatial and temporal information did not significantly improve coordination compared to their unimodal counterparts. In this specific case, the authors argued that the unimodal visual condition already displayed excellent levels of synchronization and this might have affected the multisensory integration levels when it was combined with the auditory information. Thus, it was proposed by the authors that the task difficulty might have mediated the integration of the sensory information, at least in terms of enhancing the coordination. One of the aims of the following experimentation will be to test this hypothesis by occluding one of the modalities at specific locations and amounts of the trajectory in a similar way to Experiment 1.

There is rarely a situation where sensory information from two or more modalities is available continuously without any interruption or discontinuity. Thus, the integration of information cross-modally serves a vital purpose of maintaining accurate perception and control of action in our dynamic environment. The temporary occlusion or discontinuity of one modality can be “filled-in” by another modality which acts to compensate for the missing information. Take for example a situation where a cat is chasing a mouse inside a house, as the cat chases the mouse it will navigate over/under the furniture and other obstacles, occasionally disappearing from view (e.g. the cat racing behind a couch). Despite the intermittent visual information the cat’s movements can still be tracked, even when vision is completely occluded, by integrating key auditory information relating to these movements such as the sound of the cats paws on the floor and transient sounds of the cat brushing against objects. This type of interplay between audition and vision has also been shown experimentally by Väljamäe & Soto-Faraco (2008). In their study participants were asked to judge the continuity of a series of discrete flashes increasing in depth accompanied by a series of discrete beeps the increased in loudness and were to be ignored. The individual modalities were presented at a high or low rate, corresponding to shorter and longer intervals between discrete presentations respectively. When the low rate visual stimulus was accompanied by the high rate auditory stimulus the discrete visual flashes were perceived as continuous. In this example, the auditory stimulus essentially "fills-in" the gaps between the discrete flashes creating a perception of continuity with the visual modality. These results indicate that information from another modality can compensate for the lack of information in another modifying the overall perception of these stimuli. The second aim of this experiment is to assess this "filling-in" effect with audio-visual stimuli by occluding one or both modalities.

In order to explore this "filling-in" effect three different stimuli were used with the same synchronization task as experiment 1. Similar occlusion amounts and locations as experiment 1 were used with the three different bimodal stimuli; visual occluded with auditory non-occluded, visual non-occluded with auditory occluded, both visual and auditory stimuli occluded. Based on the findings from Väljamäe & Soto-Faraco (2008), where it was shown that one modality can "fill-in" for another, it was firstly hypothesised that in the current study occlusion in both modalities would produce significantly worse performance compared to when only one modality was occluded since when both modalities are occluded it is not possible for the "filling-in" effect. Secondly, it was hypothesised that performance in the synchronization task would be better when the visual stimulus was not occluded. This is related to the fact that it is already well known that vision is superior to audition in terms of spatial perception thus it is safe to assume that this modality would be more effective at "filling-in" compared to audition.

5.4.1 Methodology

5.4.1.1 Participants

Thirteen volunteers (six females and seven males) between the age of 19 and 35 years (21.62 yrs. ±4.57) took part in the experiment. All participants were right handed, had normal or corrected to normal vision and no known history of neuromuscular deficits that would affect their participation. Colour blindness was assessed using a series of Ishihara pictures and none of the participants had any form of colour blindness. No compensation was given to the participants for their involvement in the experiment. Ethical approval was received from the Dublin City University Research Ethics Committee (DCUREC/2011/038).

5.4.1.2 Stimuli

The same stimuli from Experiment 1 were used to create three different bimodal stimuli where both modalities were occluded (bi-occlusion condition) or only one modality was occluded (uni-occlusion conditions): occluded auditory combined with non-occluded visual (A_o-V), non-occluded auditory combined with occluded visual (A-V_o) and occluded auditory combined with occluded visual (A_o-V_o). Each of the bimodal stimuli were occluded at the same locations as Experiment 1 (End, Middle and FortyFive) but in contrast to Experiment 1 only the smallest and largest Occlusion Amounts were used (80° and 160°).

5.4.1.3 Procedure

The same procedure as Experiment 1 was followed. For the familiarisation participants practiced synchronizing with a non-occluded bimodal stimulus, A-V. This bimodal stimulus consisted of the two unisensory stimuli used in the familiarisation for Experiment 1 played together. Participants had to swing to the left as the square moved left fading towards red and as the sound panned to the left ear fading towards a high pitch. Participants had to swing to the right as the square moved right fading towards yellow and as the sound panned to the right ear fading towards a low pitch. For these left and right swings participants had to synchronize the endpoint of the movements with the visual and auditory endpoints as best they could. It was emphasised that participants should maintain their focus on both stimuli for the full duration of each trial. After familiarisation, it was explained to the participants that during the main experiment the same stimulus will be presented but that one or both of the modalities will be occluded by different amounts and in different locations. Importantly, it was highlighted that the task was still to synchronize the movements of the pendulum with the stimuli, even though parts of them will be occluded.

The design of the experiment was a 3 (Stimulus Combination) × 3 (Occlusion Location) × 2 (Occlusion Amount), resulting in a total of 18 conditions. Participants completed one trial of each of the 18 randomised conditions for each of the two blocks. There was a 30 sec break after each 40 sec trial and a five minute break between blocks

5.4.1.4 Analysis

The data were processed in the same way as described in the previous method section. Similar variables were analysed and a 3 (Stimulus Combination) × 3 (Occlusion Location) × 2 (Occlusion Amount) repeated-measures analysis of variance (ANOVA) was used to assess CRP, SD CRP, Left and Right endpoint Anchoring, $AI_{spatial}$ and $AI_{temporal}$. Similar to Experiment 1, one-sample *t*-tests were used to assess CRP timing, $AI_{spatial}$ and $AI_{temporal}$. All of the *t*-tests were performed on Occlusion Amount and Occlusion Location for each of the Stimulus Combinations. The size of the effect for all of the ANOVA analysis was reported by means of the partial eta squared (η^2_p).

5.4.2 Results

5.4.2.1 Mean Continuous Relative Phase

The 3 (Stimulus Combination) × 3 (Occlusion Location) × 2 (Occlusion Amount) repeated-measures ANOVA on CRP yielded a significant main effect for Occlusion Location ($F_{2,24} = 13.05$, $p < .01$, $\eta^2_p = .52$), which showed higher CRP values with End (16.2°) compared to Middle (11.7°) and FortyFive (10.6°) Occlusion, as shown in Fig. 6. The interaction between Stimulus Combination and Occlusion Location was also found to be significant ($F_{4,48} = 3.49$, $p < .05$, $\eta^2_p = .23$). This interaction was investigated using a simple effects analysis and revealed higher CRP values for A_o-V_o (19.2°) compared to A_o-V (14.8°) and A-V_o (14.6°) only with End occlusion. It also showed that End had significantly higher CRP values than Middle and FortyFive Occlusion for all Stimulus Combinations. There were no other significant findings; Stimulus Combination ($F_{2,24} = 2.47$, $p > .05$, $\eta^2_p = .17$), Occlusion Amount ($F_{1,12} = 0.06$, $p > .05$, $\eta^2_p = .01$), Stimulus Combination and Occlusion Amount interaction ($F_{2,24} = 1.02$, $p > .05$, $\eta^2_p = .08$), Occlusion Amount and Occlusion Location interaction ($F_{2,24} = 0.46$, $p > .05$, $\eta^2_p = .04$), Stimulus Combination, Occlusion Amount and Occlusion Location interaction ($F_{4,48} = 1.95$, $p > .05$, $\eta^2_p = .14$). A one-sample *t*-test revealed that CRP was significantly different from zero for all conditions apart from A_o-V_o FortyFive. Considering that the values are negative, it indicated that participants tended to lead the stimulus in all of those conditions. Table 4 displays the results of the one-sample *t*-tests for CRP.

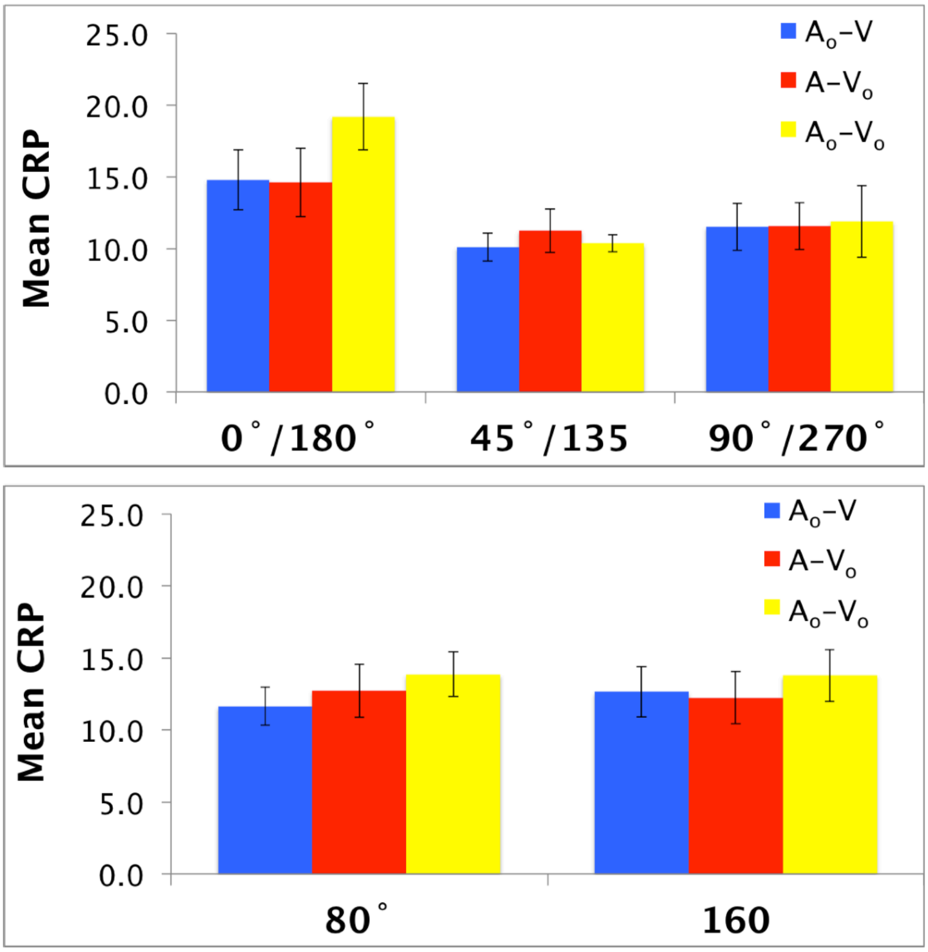

Figure 6 Mean Continuous Relative Phase

Categories	Mean	SD	t	df	Sig (2-tailed)
A_o-V End	-13.62	8.50	5.77	12	.000
A_o-V Fortyfive	-6.14	7.09	3.12	12	.009
A_o-V Middle	-9.40	7.60	4.46	12	.001
A-V_o End	-9.76	12.46	2.82	12	.015
A-V_o Fortyfive	-7.35	8.67	3.06	12	.010
A-V_o Middle	-8.68	8.15	3.84	12	.002
A_o-V_o End	-17.80	9.47	6.78	12	.000
A_o-V_o Fortyfive	-1.70	8.06	.76	12	.463
A_o-V_o Middle	-8.95	10.58	3.05	12	.010
A_o-V 80	-9.67	6.32	5.52	12	.000
A_o-V 160	-9.768	8.16	4.32	12	.001
A-V_o 80	-8.82	9.72	3.27	12	.007
A-V_o 160	-8.38	9.58	3.15	12	.008
A_o-V_o 80	-10.07	7.99	4.54	12	.001
A_o-V_o 160	-8.90	9.08	3.54	12	.004

Table 4 CRP one-sample *t*-tests

5.4.2.2 Standard Deviation of Continuous Relative Phase

The 3 (Stimulus Combination) × 3 (Occlusion Location) × 2 (Occlusion Amount) repeated-measures ANOVA on SD CRP yielded a significant main effect for Stimulus Combination ($F_{2,22} = 8.38, p < .01, \eta^2_p = .41$), revealing higher SD CRP values for A_o-V_o (6.5°) conditions compared to A_o-V (5.7°) conditions, as shown in Fig. 7. Occlusion Location was significant ($F_{2,24} = 10.40, p < .01, \eta^2_p = .46$), showing higher SD CRP values for the End (6.8°) compared to Middle (5.6°) and FortyFive (5.8°) Occlusion. The interaction between Stimulus Combination and Occlusion Location was also found to be significant ($F_{4,48} = 3.77, p < .05, \eta^2_p = .24$). A simple effects analysis revealed that for End occlusion A_o-V (5.9°) had significantly lower variability than A-V_o (6.6°) and A_o-V_o (7.8°). A-V_o also had significantly lower variability than A_o-V_o. The analysis of this interaction also revealed greater variability with End compared to both Middle and FortyFive Occlusion for the A-V_o and A_o-V_o Stimulus Combinations. The interaction between Stimulus Combination and Occlusion Amount was found to be significant ($F_{2,24} = 3.77, p < .05, \eta^2_p = .24$). A simple effects analysis revealed that A$_o$-V (5.4°) had a significantly lower variability than A-V$_o$ (6.0°) and A$_o$-V$_o$ (6.4°) for the 80° occlusion conditions. While for the 160° occlusion conditions A-V$_o$ (5.8°) had significantly less variability than A$_o$-V$_o$ (6.6°). There were no other significant findings; Occlusion Amount ($F_{1,12} = 0.65, p > .05, \eta^2_p = .05$), Occlusion Amount and Occlusion Location interaction ($F_{2,24} = 0.04, p > .05, \eta^2_p = .00$), Stimulus Combination, Occlusion Amount and Occlusion Location interaction ($F_{4,48} = 1.18, p > .05, \eta^2_p = .09$).

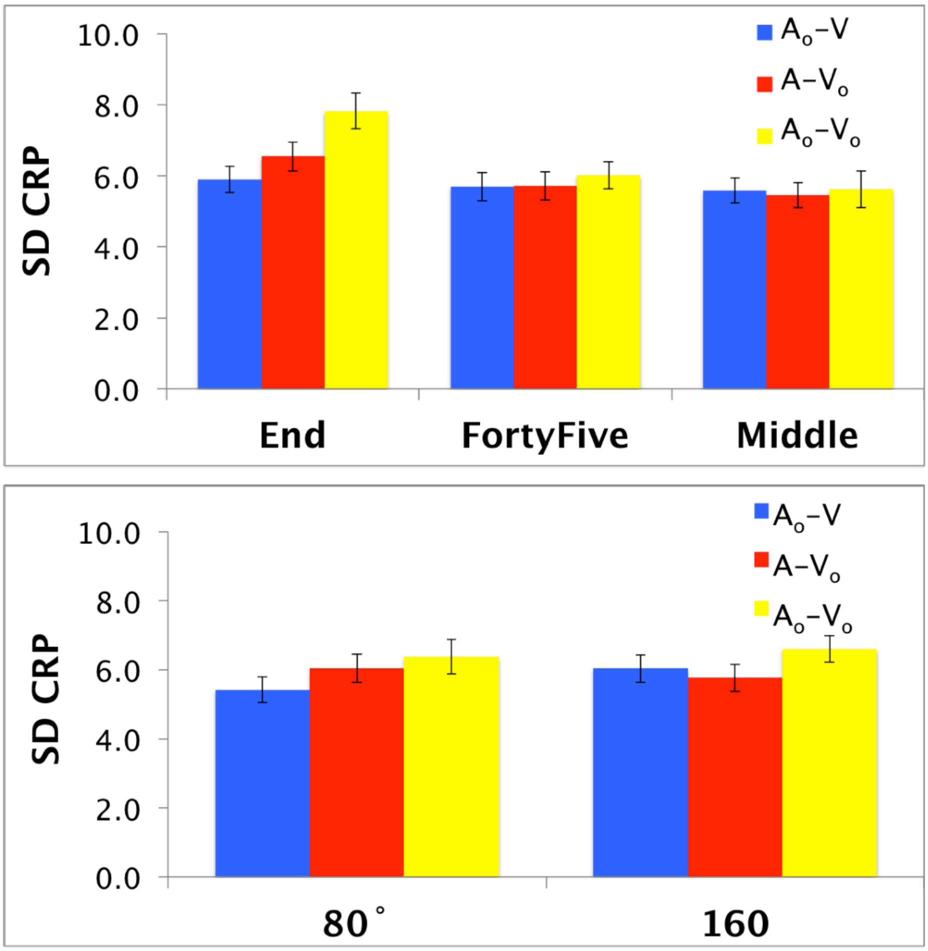

Figure 7 Standard Deviation of Continuous Relative Phase for all Conditions

5.4.2.3 Spatial Anchoring

The 3 (Stimulus Combination) × 3 (Occlusion Location) × 2 (Occlusion Amount) repeated-measures ANOVA’s performed on Left Spatial Anchoring revealed no significant results; Stimulus Combination ($F_{2, 24} = 0.70, p > .05, \eta^2_p = .06$), Occlusion Amount ($F_{1, 12} = 1.01, p > .05, \eta^2_p = .08$), Occlusion Location ($F_{2, 24} = 1.42, p > .05, \eta^2_p = .11$), Stimulus Combination and Occlusion Amount interaction ($F_{2, 24} = 1.31, p > .05, \eta^2_p = .10$), Stimulus Combination and Occlusion Location interaction ($F_{4, 48} = 0.95, p > .05, \eta^2_p = .07$), Occlusion Amount and Occlusion Location interaction ($F_{2, 24} = 0.02, p > .05, \eta^2_p = .00$), Stimulus Combination, Occlusion Amount and Occlusion Location interaction ($F_{4, 48} = 0.91, p > .05, \eta^2_p = .07$). The 3 (Stimulus Combination) × 3 (Occlusion Location) × 2 (Occlusion Amount) repeated-measures ANOVA's performed on Right Spatial Anchoring also revealed no significant results; Stimulus Combination ($F_{2, 24} = 0.97, p > .05, \eta^2_p = .08$), Occlusion Amount ($F_{1, 12} = 0.18, p > .05, \eta^2_p = .01$), Occlusion Location ($F_{2, 24} = 0.58, p > .05, \eta^2_p = .05$), Stimulus Combination and Occlusion Amount interaction ($F_{2, 24} = 0.68, p > .05, \eta^2_p = .05$), Stimulus Combination and Occlusion Location interaction ($F_{4, 48} = 0.90, p > .05, \eta^2_p = .07$), Occlusion Amount and Occlusion Location interaction ($F_{2, 24} = 0.21, p > .05, \eta^2_p = .02$), Stimulus Combination, Occlusion Amount and Occlusion Location interaction ($F_{4, 48} = 0.84, p > .05, \eta^2_p = .07$). This indicates that the modifications made to all three Stimulus Combinations in terms of Occlusion Location and Occlusion Amount had no significant impact on the spatial structure of the participant's movement, namely the ability to anchor movement at the reversal points. The Spatial Anchoring values displayed in Fig. 8 are averaged across left and right.

$AI_{Spatial}$ was analysed using a one sampled *t*-test and the values for each condition are presented in Fig. 8. The results revealed that all conditions were significantly less than 0.5, indicating more anchoring on the left than the right endpoint, apart from A_o-V End, A-V_o FortyFive and A_o-V_o FortyFive. Table 5 displays the results from the one-sample *t*-tests for $AI_{Spatial}$.

Categories	Mean	SD	t	df	Sig (2-tailed)
A_o-V End	.47	.05	-2.13	12	.055
A_o-V Fortyfive	.44	.05	-3.88	12	.002
A_o-V Middle	.45	.05	-3.52	12	.004
A-V_o End	.46	.06	-2.65	12	.021
A-V_o Fortyfive	.47	.06	-1.90	12	.082
A-V_o Middle	.46	.06	-2.48	12	.029
A_o-V_o End	.45	.04	-4.39	12	.001
A_o-V_o Fortyfive	.48	.07	-1.23	12	.243
A_o-V_o Middle	.44	.05	-4.58	12	.001
A_o-V 80	.45	.06	-2.71	12	.019
A_o-V 160	.46	.03	-4.85	12	.000
A-V_o 80	.47	.05	-2.39	12	.034
A-V_o 160	.46	.05	-2.93	12	.013
A_o-V_o 80	.46	.04	-3.21	12	.008
A_o-V_o 160	.45	.05	-3.57	12	.004

Table 5 $AI_{Spatial}$ one-sample *t*-tests

5.4.2.4 Temporal Anchoring

The 3 (Stimulus Combination) × 3 (Occlusion Location) × 2 (Occlusion Amount) repeated-measures ANOVA on Temporal Anchoring Left yielded a significant main effect for Stimulus Combination ($F_{2,24} = 12.04$, $p < .01$, $\eta^2_p = .50$), revealing more anchoring with A_o-V (24.7 ms) compared to A_o-V_o (28.7 ms) conditions, as shown in Fig. 8. There was also a significant main effect for Occlusion Location ($F_{2,24} = 8.32$, $p < .01$, $\eta^2_p = .41$), which showed more anchoring with Middle (24.6 ms) compared to End (28.6 ms) Occlusion. The interaction between Stimulus Combination and Occlusion Location was significant ($F_{4,48} = 4.28$, $p < .01$, $\eta^2_p = .26$) and a simple effects analysis revealed that for the End occlusion there was significantly more temporal anchoring with A_o-V (23.4 ms) compared to A-V_o (29.2 ms) and A_o-V_o (33.3 ms). This analysis of the interaction also revealed differences between each Stimulus Combination for Occlusion Location. For A_o-V, End (23.4 ms) had more anchoring than FortyFive (26.5 ms) occlusion, for A-V_o, Middle (23.5 ms) had more anchoring than both End (29.2 ms) and FortyFive (26.8 ms) occlusion, while for A_o-V_o, both Middle (26.0 ms) and FortyFive (26.8 ms) had more anchoring than End (33.3 ms) occlusion. There were no other significant findings; Occlusion Amount ($F_{1, 12}$ = 1.77, p > .05, η^2_p = .13), Stimulus Combination and Occlusion Amount interaction ($F_{2, 24}$ = 2.82, p > .05, η^2_p = .19), Occlusion Amount and Occlusion Location interaction ($F_{2, 24}$ = 0.36, p > .05, η^2_p = .03), Stimulus Combination, Occlusion Amount and Occlusion Location interaction ($F_{4, 48}$ = 0.68, p > .05, η^2_p = .05). A planned simple effects analysis for Stimulus Combination and Occlusion Amount revealed that for the 80° Occlusion A_o-V (22.9 ms) had significantly more temporal anchoring compared to A-V_o (27.2 ms) and A_o-V_o (27.8 ms) and for the 160° occlusion conditions both A_o-V (26.5 ms) and A-V_o (25.8ms) had significantly more anchoring than A_o-V_o (29.7 ms).

The 3 (Stimulus Combination) × 3 (Occlusion Location) × 2 (Occlusion Amount) repeated-measures ANOVA on Temporal Anchoring Right stimulus yielded a significant main effect for Stimulus Combination ($F_{2, 24}$ = 12.94, P < .01, η^2_p = .52) indicating that A_o-V (24.7 ms) had significantly more temporal anchoring than both A-V_o (27.2 ms) and A_o-V_o (28.9 ms). The significant findings for Occlusion Location ($F_{2, 24}$ = 9.12, p < .01, η^2_p = .43) were the same as those found with Temporal Anchoring Left. There was a significant interaction found between Stimulus Combination and Occlusion Location ($F_{4, 48}$ = 3.38, p < .05, η^2_p = .22) and a simple effects analysis revealed the same findings as reported with Temporal Anchoring Left. There was also a significant interaction found between Stimulus Combination and Occlusion Amount ($F_{2, 24}$ = 4.61, p < .05, η^2_p = .28). A simple effects analysis revealed the same findings reported from the planned simple effects analysis for Temporal Anchoring Left. Additionally, this interaction revealed that for the A_o-V Stimulus Combination only there was significantly more temporal anchoring for the 80° occlusion (22.7 ms) compared to the 160° occlusion (26.7 ms) conditions. There were no other significant findings; Occlusion Amount ($F_{1, 12}$ = 2.32, p > .05, η^2_p = .16), Occlusion Amount and Occlusion Location interaction ($F_{2, 24}$ = 0.14, p > .05, η^2_p = .01), Stimulus Combination, Occlusion Amount and Occlusion Location interaction ($F_{4, 48}$ = 0.66, p > .05, η^2_p = .05).

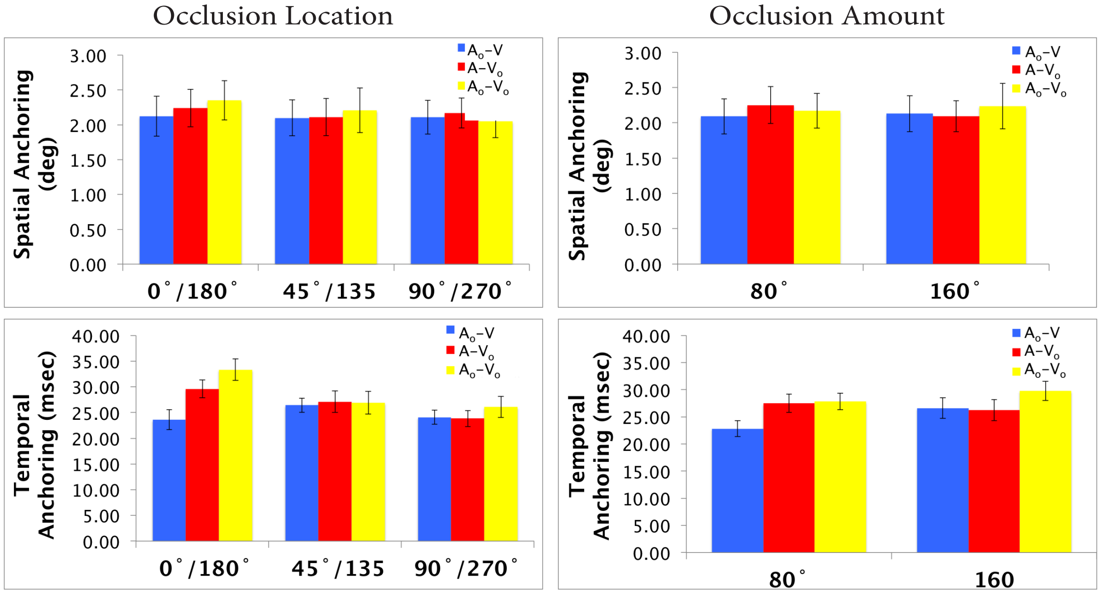

Figure 8 Mean Spatial and Temporal Anchoring values for all conditions

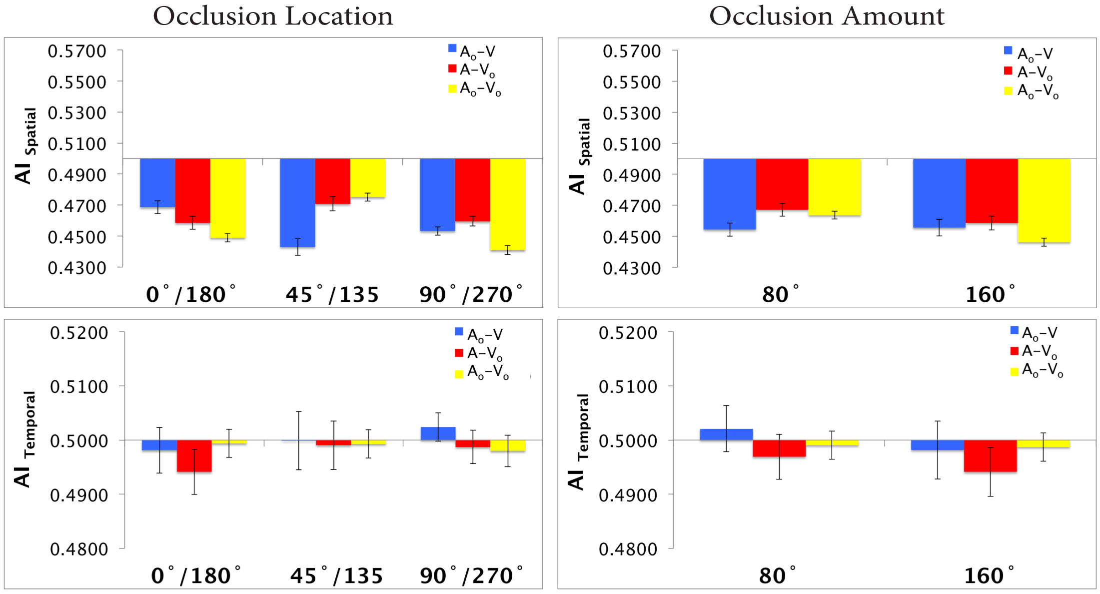

Figure 9 Mean Spatial and Temporal Anchoring index for all conditions

$\text{AI}_{\text{Temporal}}$ was analysed using a one sampled *t*-test and the values for each condition are presented in Fig. 9. The results revealed that only A-V_o 160° differed significantly from 0.5, indicating more anchoring on the left than the right endpoint. This result indicates that the modifications to Occlusion Location and Occlusion Amount did not create a bias in terms of temporal anchoring between the left and right endpoints except with A-V_o 160°. Table 6 displays the results from the one-sample *t*-tests for $AI_{Temporal.}$

Categories	Mean	SD	t	df	Sig (2-tailed)
A_o-V End	.50	.02	-.45	12	.661
A_o-V Fortyfive	.50	.02	-.02	12	.985
A_o-V Middle	.50	.01	.92	12	.375
A-V_o End	.50	.02	-1.27	12	.228
A-V_o Fortyfive	.50	.02	-.67	12	.517
A-V_o Middle	.50	.01	-1.69	12	.118
A_o-V_o End	.50	.01	-.24	12	.813
A_o-V_o Fortyfive	.50	.01	-.28	12	.785
A_o-V_o Middle	.50	.01	-.70	12	.500
A_o-V 80	.50	.01	.58	12	.575
A_o-V 160	.50	.02	-.42	12	.683
A-V_o 80	.50	.01	-.81	12	.434
A-V_o 160	.49	.01	-2.50	12	.028
A_o-V_o 80	.50	.01	-.44	12	.666
A_o-V_o 160	.50	.01	-.38	12	.710

Table 6 $AI_{temporal}$ one-sample *t*-tests

5.5 General Discussion

5.5.1 Occlusion and Multisensory Stimuli

While occlusion has been used to examine the specific parts of a visual stimulus' trajectory that are essential for catching and juggling (Amazeen et al. 1999; Sánchez García et al. 2013; Fine et al. 2014) Experiment 2 added a novel approach to the use of occlusion by investigating the integration of auditory and visual information when one or both of these modalities were occluded by different amounts and at different locations. Globally, the results indicated that regardless of whether only one or both modalities were occluded when the endpoints were no longer visible coordination was significantly lower. As mentioned previously in Experiment 1 one of the possible explanations for these observed differences may relate to the difference occlusion times for End and the other two occlusion locations. Importantly, it was also shown that the level of coordination significantly improved when only one modality was occluded compared to when both were occluded. The results also highlighted that in terms of stabilising coordination perceiving relative direction at the endpoints of the visual stimulus seemed to be a key factor. Overall, the results seemed to hint at evidence of sensory integration and the exact nature of this integration will be discussed below.

The results from the CRP analysis indicated that for all stimulus combinations synchronization was significantly lower for End compared to Middle and FortyFive Occlusion Locations. More specifically, results relating to End occlusion revealed that synchronization was negatively affected when both modalities were occluded (A_o-V_o) compared to conditions where only one modality was occluded (A_o-V & A-V_o). Interestingly, for all Occlusion Locations there were no differences between CRP values for A_o-V and A-V_o, which could imply that in these conditions the non-occluded modality served to "fill-in" for the occluded information. This "filling-in" effect seems to be present for both modalities. Based on previous research showing that participants tend to rely more on the visual information compared to the auditory information for this type of task (Armstrong and Issartel 2014), one could assume that when the reliability of visual information was reduced (i.e. occluded), participants will still perform better than when the reliability of auditory information was reduced. The results show that there were no differences between A_o-V and A-V_o for End occlusion. Thus, based on these findings, it seems that the participants did not rely solely on the visual modality and instead integrated the information from both modalities.

Despite these findings, the interpretation of the results remains complex as key differences between the Stimulus Combinations were found in terms of stability of the coordination. Regarding the SD CRP findings, even though both uni-occlusion conditions were significantly more stable than the bi-occlusion condition it appeared that the visual modality was more effective at “filling-in” for the occluded auditory modality than vice versa for the uni-occlusion conditions. These results are important since they highlight that audio and visual information are integrated differently depending on which modality is occluded. Namely, the high spatial saliency with the visual modality provides strong support for stabilising the coordination when an auditory stimulus is occluded at the endpoints and while the auditory modality can also “fill-in” for an occluded visual stimulus it is less effective. Further research may be required in order to investigate whether this effect can be reversed in favour of the auditory modality when the stimulus is purely based on timing information (i.e. no spatial information is present), since audition is more accurate with temporal information compared to vision (Kato and Konishi 2006). Globally, the results indicate that the presence of a non-occluded modality, as in the uni-occlusion conditions, significantly improved coordination when compared to conditions where both modalities were occluded. However, the results point towards a heavier weighting of the visual modality in the integration of this sensory information when it comes to the stability of the coordination.

The analysis of temporal anchoring revealed interesting differences in the effect of Occlusion Location compared to the results from CRP and SD CRP. Overall, the results for both left and right temporal anchoring indicated more accurate timing with Middle compared to End Occlusion. This result provides further support for the previously discussed importance of perceiving relative direction at the endpoints. However, when these results were analysed for each individual Stimulus Combination they revealed deviations from the previously reported trend. For the uni-occlusion conditions when the auditory modality was occluded (A_o-V) there was more temporal anchoring for End compared to FortyFive occlusion. This is similar to the results from Experiment 1 for A_o where temporal anchoring was similar for End and FortyFive occlusion which was attributed to the unusual sound the was created with this type of occlusion. Thus, the results from A_o-V may be explained by the integration of this unusual auditory condition that interfered with coordination and had a negative effect on timing at the endpoints.

Importantly, for End occlusion A_o-V had more anchoring than both A-V_o and A_o-V_o. This result and the fact that A-V_o was not different from A_o-V_o implies that there may be a heavier weighting on the visual modality, at least in terms of endpoint timing. This might be due to the fact that relative direction is very salient at these points for a visual stimulus. Additionally, it should be noted that these results indicate that the auditory modality did not appear to help stabilise endpoint timing when the visual modality was occluded at the endpoints. These results coupled with those from CRP and SD CRP indicate that while globally in the uni-occlusion conditions the modalities appear to be integrated (see CRP results), in terms of the stability of coordination and endpoint timing a visual bias still persists in these conditions. These differences between the two modalities in terms of “filling-in” for an occluded stimulus may be related to differences in perceiving spatial information since vision is superior to audition in this domain (Alais and Burr 2004). As a consequence of this poor spatial perception with audition the ability to perceive relative direction would be poor also and may have limited the ability of the auditory stimulus to “fill-in” for the occluded visual stimulus.

There was a significant reduction in temporal anchoring for A_o-V when occlusion was increased from 80° to 160°, indicating that endpoint timing was more accurate for smaller amounts of occlusion. This result appears to indicate that participants did integrate the auditory and visual stimuli. If participants only relied on the visual modality then no changes between the occlusion amounts would be expected. It is important to note that despite this negative effect on endpoint timing when occlusion was increased, even with a large amount of occlusion A_o-V still had more temporal anchoring than A_o-V_o. Thus, it would appear that the occlusion of auditory information, specifically with 160° occlusion, resulted in a decrease in performance as the task difficulty increased, showing that sensory information was integrated with this stimulus.

It is known that information from different modalities can be effectively integrated to improve coordination when presented closely together in space and time. On the other hand, when the sensory information does not coincide, a reduction in the level of coordination can emerge (Carson and Kelso 2004). Thus, one could argue that for A_o-V the sensory information could be effectively integrated with 80° occlusion but when the occlusion increased to 160° the two modalities became perceived as spatially and temporally incongruent resulting in a significant decrease in the amount of anchoring. This relates closely to the idea that sensory information can only be integrated within a given temporal window (Alais et al. 2010) and that in the current study for 160° occlusion the modalities may have been outside of this window of integration.

Despite this finding it is important to note that for 160° occlusion both A_o-V and A-V_o had significantly more temporal anchoring than A_o-V_o leading to another possible view that the integration of these sensory modalities is mediated by the task difficulty. The results relating to Occlusion Amount indicate that the integration of the modalities in the uni-occlusion conditions differs depending on the Occlusion Amount. While for 80° occlusion A_o-V had significantly more temporal anchoring than A-V_o and A_o-V_o, when the occlusion increased to 160° both A_o-V and A-V_o were at similar levels and both had more anchoring than A_o-V_o. Overall this implies that when the discrepancy between the modalities is small, as with 80° occlusion, there may be a visual bias but as this discrepancy between the modalities increases the auditory modality appears to be as effective as the visual modality for stabilizing timing. This was also supported by findings relating to the stability of coordination at different Occlusion Amounts. While for 80° occlusion A_o-V was more stable than A-V_o and A_o-V_o when the Occlusion Amount increased to 160° the two uni-occlusion stimuli had similar levels of stability and A_o-V was only significantly more stable than A_o-V_o. This mirrors the temporal anchoring findings and indicates that the ability of a modality to fill-in for occlusion in another modality is different for auditory and visual information.

Additionally, these results may imply that task difficulty mediates sensory integration since at 160° occlusion both uni-occlusion conditions were equally effective at improving timing compared to the bi-occlusion conditions. Importantly, the endpoint timing for the visual modality from Experiment 1 got worse as Occlusion Amount increased from 80° to 160° and this trend disappeared when this same visual stimulus was coupled with auditory information, as in A-V_o. Also, the coordination with A-V_o remained at the same level as Occlusion Amount increased for both SD CRP and temporal anchoring and implies that the auditory modality was effectively integrated in order to stabilise coordination across a variety of Occlusion Amounts. Taken together these results provide a strong indication that the auditory modality effectively helped to stabilise the coordination possibly by “filling-in” for the missing visual information. Even though the evidence seems to point towards sensory integration further research is needed in order to establish the relative weighting of the two sensory modalities in this multisensory integration process and whether the perception of relative direction with the auditory modality played a role in stabilising coordination when it was integrated with an occluded visual stimulus.

Globally, the results from Experiment 2 supported the Gibsonian perspective of perception and action. The improved synchronization observed with the uni-occlusion compared to bi-occlusion conditions when the endpoints were occluded clearly supports the general theory of perception and action put forward by Gibson. This result implies that in the uni-occlusion conditions both the auditory and visual modalities were able to “fill-in” for the occluded modality, helping to stabilise to synchronizing compared to when both modalities were occluded. Drawing on the work by Gibson (1986) this would be expected since his theory places an importance on the overall information provided by a stimulus. In these uni-occlusion conditions information relating to the full trajectory of the stimuli was always available since one of the modalities was always un-occluded. Thus by integrating the information from these two modalities the flow of information specifying the trajectory of the overall stimulus was continuous. The difference between the uni-occlusion and bi-occlusion conditions supports Gibson's theory of perception and action since there was less task-relevant information available in the bi-occlusion conditions because no information relating to relative direction at the endpoints was provided. Within the two uni-occlusion conditions it was found that the visual modality appeared to be more effective than the auditory modality at "filling-in". As mentioned previously the saliency issues with the information provided by the auditory modality may have led to this observed difference. In other words the information provided by the visual modality for A_o-V, specifically at the endpoints, was more salient and task-relevant that the information provided by the auditory modality for A-V_o at the same location. This supports Gibson's theory since the basis of his approach to perception and action is that information is specific and meaningful for a given action, thus a lack of task-relevant or saliency of information will have a negative impact on synchronization.

5.5.2 Unimodal versus Multimodal

The comparison of the results between Experiment 1 and 2 is useful in terms of understanding whether the multimodal conditions actually enhanced synchronization. As expected there is a clear benefit of having the visual modality present when the auditory stimulus is occluded (A_o-V) compared to when only occluded auditory information is available (A_o) as the non-occluded visual modality is quite salient in terms of spatial information. Regarding the Visual conditions, a clear difference between A-V_o (Exp. 2) and V_o (Exp. 1) would indicate a bimodal benefit since the only difference between these two conditions is the addition of auditory information in the former. While CRP and SD CRP results were similar for V_o and A-V_o differences did occur with regards to the anchoring results. The results from both spatial and temporal anchoring appeared to indicate more anchoring in A-V_o

compared to V_o. In Experiment 1 the spatial anchoring values were very similar for V_o across all occlusion locations and amounts (mean Left and Right = 3.3°) while for A-V_o in Experiment 2 these values appear to drop by over 1 degree (mean Left and Right = 2.2°). The comparison of temporal anchoring provides further evidence. There appears to be a clear improvement in anchoring of nearly 5 ms when V_o (mean Left and Right = 31.6 ms) is compared with A-V_o (mean Left and Right = 26.9 ms), which indicates that auditory information appears to "fill-in" for the occluded visual stimulus. The strong support for this bimodal benefit with temporal anchoring makes sense since the auditory modality is particularly salient within the temporal domain (Repp 2005).

Importantly these results appear to indicate that the integration of multisensory information may to be mediated by task difficulty. When the visual modality was occluded the auditory information, specifically at the endpoints, appeared to help stabilize the timing of the pendulum swings at these locations. Armstrong and Issartel (under review) conducted an experiment assessing the same bimodal stimulus without any occlusion (A-V) and their results indicated that synchronization was similar to the unisensory visual condition (V) implying that no bimodal benefit occurred when the modalities were presented together. When compared with the results from the current study it seems clear that integration between different sensory modalities is somewhat dependent on the task difficulty. In Armstrong & Issartel the task may not have necessitated the same level of sensory integration since the visual modality already provided enough information to effectively stabilise the coordination and produce a high level of performance. In the current study, the reliability of the visual modality was reduced and the perception-action coupling weakened, thus the task difficulty may have necessitated the integration of the available auditory information in order to enhance the coordination. It is also unclear whether the perception of relative direction with the auditory modality played a role in the integration with the occluded visual stimulus. Further research is required in order to address these questions relating to relative direction and task difficulty.

The use of occlusion with a multisensory stimulus represents an important step towards assessing synchronization with environmental stimuli that are more representative of everyday stimuli. Rhythms in daily life are generally not completely continuous and often contain many disruptions that affect the perception-action coupling. In general, research mainly focuses on using computer-generated stimuli that lack key characteristics found in a real life environment. However, recent research articles have been moving towards more realistic stimuli and characteristics. Examples can be found across a range of methodologies such as assessing synchronization with visual stimuli that have the velocity profile of biological motion (Kilner et al. 2007) and the use of more spatially compatible visual stimuli, such as a bouncing ball or images of a finger raising and lowering, in finger tapping studies (Hove et al. 2010; Hove et al. 2013). Importantly, the move towards understanding interpersonal coordination as seen with a large number of studies investigating this area (e.g. Issartel, Marin, & Cadopi, 2007; Lagarde, 2013; Marin & Issartel, 2009; Noy, Dekel, & Alon, 2011; Richardson et al., 2007; Richardson, Marsh, & Schmidt, 2005; R. Schmidt & O'Brien, 1997; Varlet, Marin, Lagarde, & Bardy, 2011) is an essential part of understanding how we interact with others in daily life and represents an extremely useful way of assessing synchronization with "ecological" stimuli (i.e. other humans moving). In the current study, Experiment 1 and 2 attempted to create somewhat more realistic multisensory stimuli by partially occluding one or both of the modalities. Future research may look to expand on this methodology by making these stimuli even closer to what one typically experiences in daily life perhaps by modifying the predictability of occlusion.

5.6 Conclusion

Overall the results from Experiment 1 appear to indicate that while the perception of relative direction is important for both vision and audition the latter modality appears to be more sensitive to the removal of this information. This sensitivity of audition to occlusion may reflect the difficulty in perceiving spatial information with this modality. In contrast, the strength of the visual modality in the spatial domain may have led to the observed resilience of the perception-action system when the endpoints were occluded. Despite this resilience the perception of relative direction at the endpoints of the visual modality was still an essential part of the perception-action coupling since coordination was significantly reduced when these locations were occluded. These results provide support for the perceptual basis of coordination with visual stimuli, which emphasises the importance of information in stabilising coordination, specifically, information at the reversal points of the stimuli. Previous research has indicated that the supplementation of spatial information (i.e. providing information about relative direction) did not improve synchronization with an auditory stimulus (Armstrong and Issartel, under review). Despite this, the results from the current experiment show that the perception of relative direction, specifically at the reversal points of a moving stimulus, is critical for synchronization with auditory stimuli.

The second experiment aimed at assessing how the integration of sensory information with visual and auditory stimuli is affected when one or both of the modalities are occluded. Overall the results seemed to indicate that synchronization was enhanced for the uni-occlusion conditions compared to the bi-occlusion condition. The results indicated that as the task difficulty increased (increasing Occlusion Amount) the two uni-occlusion conditions appeared to both provide a similar benefit when compared to the bi-occlusion condition. This hints towards a demonstration of sensory integration with these two modalities and may imply that the perception of relative direction in the non-occluded modality played a role in stabilising coordination. Along those lines, the comparison between V_o (Exp. 1) and A-V_o (Exp. 2) seems to indicate that the coordination improved when both auditory and visual stimuli were present even when the visual modality was occluded. Overall, this indicates that task difficulty may mediate the integration of multisensory information in comparison to their unisensory counterparts but further research is required to modify the task difficulty while moving towards more ecological stimuli.

5.7 Funding source

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Chapter 6: General Discussion

6.1 Overview of thesis

Researchers within the field of perception-action have studied the interactions between an individual and it's environment. Information that is perceived by the individual plays a key role in the dynamics of this interaction and helps to support their actions. The role of information in perception-action is central to both the ecological and dynamical systems approach to understanding how we synchronize our actions with the environment. Gibson's ecological approach placed a strong emphasis on understanding the qualitative nature of information, from the environment, that is used to support action (Williams et al. 1999). Similarly, Kelso's dynamical systems approach to perception-action emphasised that "the couplings between things are informational" (Kelso 1995 p. 156) and that this information is essential for understanding the dynamics of coordination (Kelso 1995).

Many researchers have focused on the perceptual basis for motor coordination by exploring the role that information plays in perception-action. Based on the theoretical foundations mentioned above many researchers have argued and provided evidence that the coupling constraining rhythmic coordination is informational (Bingham et al. 1999; Zaal et al. 2000; Bingham et al. 2001; Bingham 2004; Roerdink et al. 2005; Schmidt et al. 2007; Richardson et al. 2007). The focus of this thesis followed the same line of thinking expressed by these studies and aimed at addressing this perceptual basis for motor coordination with auditory and visual stimuli. The three studies, in this thesis, focused on the specific information from auditory and visual stimuli that is used to help stabilise coordination.

Study 1 (Chapter 3) addressed the role of spatial information in the ability to synchronize with visual stimuli. Participants synchronized wrist-pendulum movements with a temporal stimulus, presented as a stationary square that faded between a black and green colour, and a spatio-temporal stimulus, presented as a horizontally oscillating square. Based on the results, it seems that stable coordination is still possible when no spatial information is available (temporal stimulus) but that the supplementation of spatial information (spatio-temporal stimulus) significantly improves coordination. This indicated that spatial information plays a key role in stabilising synchronization with a visual stimulus. Additionally, these results also provided support for the Perceptually Driven Dynamical model (Bingham 2004), implying that the availability of information relating to relative direction, i.e. spatial information, was an important factor in improving synchronization.

The purpose of Study 2 (Chapter 4) was to expand on the findings from Study 1 with two main objectives. Firstly, Study 2 explored whether spatial information also played an important role in stabilising synchronization with an auditory stimulus. This question was addressed by asking participants to synchronize wrist-pendulum movements with auditory and visual stimuli that contained temporal and spatio-temporal information. The results, relating to the auditory conditions, revealed that the supplementation of spatial information did not significantly improve synchronization perhaps due to the fact that audition is quite poor at perceiving information in the spatial domain. On the other hand, the results from the visual conditions supported the previous findings from Study 1 indicating that the supplementation of spatial information significantly improved synchronization with this modality. The second aim of the study was to assess how spatial information may affect the integration of these two modalities when they are presented simultaneously (bimodal conditions). In contrast to previous research the results indicated only a limited bimodal benefit, implying that performance in the bimodal conditions was not significantly better compared to their unisensory counterparts. More specifically, the bimodal conditions displayed a strong bias towards the visual modality indicating that participants mainly used this modality to control their actions.

Study 3 (Chapter 5) was based on the idea that the perception of relative direction is an important part of rhythmic coordination. The first experiment aimed to explore the role of perceiving relative direction in auditory and visual stimuli. Participants synchronized with spatio-temporal auditory and visual stimuli presented in unimodal conditions. The availability of information relating to relative direction was modified by occluding these stimuli in different locations and by different amounts. The results indicated that information relating to the perception of relative direction at the endpoints of a stimulus' trajectory is important for both modalities. However, while synchronization was still possible with the visual stimulus when the endpoints were occluded, with the auditory modality this same occlusion had a detrimental effect on synchronization. The second experiment investigated whether a non-occluded stimulus could "fill-in" for another modality that is partially occluded. Participants synchronized with audio-visual (bimodal) stimuli where one or both of the modalities were occluded in different locations and by different amounts. Overall, the results indicated that synchronization significantly improved when a non-occluded modality was present, indicating that the "filling-in" effect may have occurred in these conditions.

6.2 Possible practical implications of findings

The main findings from this thesis serve to improve our understanding of perception and action with simple motor skills at a fundamental level. Due to fundamental focus of this thesis the results may not be directly applied to “real-life” or more ecological situations. However, the results from this thesis may act as foundation that future research may be able to build on. The findings from Chapter 3 and Chapter 4 relating to the unimodal stimuli may serve as a useful platform in the development of warning or guiding signals that may help to improve safety in vehicles or improve rehabilitation. In the context of this thesis the key differences found between the visual and auditory stimulus may be useful in terms of selecting the most appropriate modality for these warning signals. It was highlighted in this thesis that the auditory modality produced worse synchronization performance compared with the visual modality when presented as continuous stimuli and previous research has shown that with discrete stimuli the opposite effect is typically found where audition is better than vision (Varlet et al. 2012). Thus, depending on the type of signal that is being developed this research may help in the appropriate selection. For example with a guidance signal, which could be used to assist stroke patients during rehabilitation, a continuous and spatially orientated stimulus may be important. Thus, based on the findings from this study a continuous spatio-temporal visual stimulus would be effective as a guiding signal. Whereas if a warning signal was being developed, timing may be crucial thus based on previous research a discrete auditory stimulus may be more effective than a continuous visual stimulus.

However it must be noted here that the findings from this thesis may only serve as a guide for exploring these type of warning or guidance signals since it is possible that the same stimulus used in this thesis used with a more complex task (i.e. more degrees of freedom) may not produce the same results due to changes in the constraints placed on the perception-action coupling. In a similar way the research findings relating to the multisensory stimuli may not be directly applied. Rather, these results serve to inform future fundamental research that will aim to develop more effective multisensory stimuli in terms of enhancing synchronization performance and more generally improve our basic understanding of how we perceive and act (some of these future research directions are discussed below is section 6.3). One of the possible applications of the findings from the multisensory aspect of this thesis relates to learning. While the multisensory stimuli in this thesis did not appear to have any benefit in terms of enhancing synchronization performance it did serve to show how changes in the type of information presented in these stimuli may affect synchronization. Understanding how we synchronize with different type of multisensory stimuli is a key element of developing an effective and efficient program for motor learning. It is possible that similar multisensory stimuli may be used in more ecological settings to improve the time it takes to learn a specific motor skill since previous research has shown that synchronization with these type of stimuli is generally significantly better than with unisensory stimuli. For example, a stroke patient who is re-learning basic motor skills may benefit from appropriate multisensory cues by providing more effective information that may be used to guide and correct movement patterns. Again the findings from this thesis only serve as a base for understanding how we synchronize with multisensory stimuli and further research is needed in order to develop a multisensory stimulus that may be appropriate for rehabilitation.

6.3 Directions of future research

6.3.1 The role of the task

The use of different tasks in studies assessing similar questions relating to perception-action often presents difficulties when comparing their findings. Comparisons between these studies often reveal contrasting results. For example, studies employing a wrist-pendulum task have found that synchronization performance with a discrete auditory stimulus and a continuous visual stimulus (no spatial information) appear to be similar (Varlet et al. 2012). In contrast, a study using similar stimuli but with a finger-tapping task found that a discrete auditory stimulus was significantly better than a continuous visual stimulus. Differences are also found in terms of the tendency to follow or lead the stimulus. For pendulum swinging participants tend to follow a discrete stimulus and lead a continuous one however with finger tapping the tendency is to precede all stimuli regardless of continuity. While it has been highlighted that differences between these two types of tasks may be due to different synchronization processes (Torre and Balasubramaniam 2009) further research directly comparing these two tasks is needed. The role of temporal and spatial congruency between the stimuli and task may also be an important factor for coordination dynamics. Studies addressing these questions will not only facilitate comparisons between studies but also help to expand our understanding of how the type of task can modify the integration of perceptual information.

6.3.2 Towards Biological Stimuli

One of the limitations of using computer-generated stimuli is that they are often far removed from what is perceived in every day life. In general, the stimuli presented to participants are perfect sinusoidal trajectories with no natural variability and a high level of predictability. Thus, it seems important for future research to move towards more realistic stimuli for participants. Several studies have begun to introduce such stimuli: images of a finger raising and lowering (Hove et al. 2010) or a bouncing ball metronome (Hove et al. 2013) with finger tapping. In line with the previous section, a direct comparison with this finger tapping task and a continuous task, such as the one used in the thesis, would be interesting to implement in order to establish how the use of more realistic stimuli impacts on synchronization. Future research may look to see if synchronization performance can be enhanced when images of a pendulum swinging back and forth are displayed to participants compared to a horizontally oscillating square. Since this stimulus would be more closely related to the task it is possible that it may be perceived differently and possibly improve synchronization.

Underpinning this idea that more realistic or "biological" stimuli may enhance synchronization performance is brain research that has discovered a strong neurological link between perception and action. Research from nearly two decades ago found that neurons in a specific area of the premotor cortex of monkeys were discharged or active when the monkey performed an action and also when it observed a similar action made by another monkey (Rizzolatti et al. 1996). These type of neurons were coined as "mirror neurons" since it appeared that the same activity was present in the brain both when an action was performed and observed. Because the same activity appears to be present during perception (observation) and action these mirror neurons have helped to solidify the intrinsic link between action and perception (Kilner et al. 2007). Research with humans has also shown that these mirror neurons may also exist. A study by Callan et al. (2010) found activity in the premotor cortex of participants' brains for both perception and production auditory tasks.

Research examining movement performance has also indicated that mirror neurons may play an important role in terms of how we perform movements. In their study Kilner, Paulignan, & Blakemore (2003) asked participants to move their arm while observing an incongruent movement that was performed by either a robot or another human. Interestingly, their results indicated that only the human making incongruent movements significantly interfered with the participant's ability to perform the correct movement. The authors concluded that these results suggest the same neural network is activated during production and observation of a human movement, which caused the observed interference. Further research examining similar movements and research questions found that observations of a human or a ball are processed differently (Kilner et al. 2007). Importantly, this research also found that the velocity profile of the incongruent human movement was a critical element of the visual information that led to an interference with the participants' movements. This is important as it gives some insight into the specific information contained within human or "biological" stimuli that can influence action, possibly through activation of mirror neurons.

Based on this research it is plausible that providing participants with more realistic or "biological" stimuli may help to improve synchronization performance by employing these mirror neurons that appear to be active during observation of a similar movement. Thus, it is important that research continues to explore how mirror neurons may affect perception-action coupling through the use of more realistic or biological stimuli. Based on this approach, future research may aim to create stimuli that replicate the synchronization movement that is to be performed using both non-human and human movement data. The use of biological motion and indeed humans acting as external stimuli has been mainly limited to the visual modality. Thus, future research may look to assess how we perceive and integrate auditory information that contains biological motion. For example, it would be interesting to see if the visual entrainment found between-persons in unintentional studies (Schmidt and O'Brien 1997; Richardson et al. 2005) can also be found when visual information is replaced by auditory stimuli (i.e. subjects can hear another person's pendulum movements). This has yet to be assessed in the literature and represents an important step in addressing the differences in unintentional coordination with biological visual and auditory stimuli.

6.3.3 Occlusion and sensory weighting

The use of occlusion in the first experiment of Study 3 was quite novel and helped to identify that information at the endpoints of the stimulus' trajectory are essential for both visual and auditory stimuli. However, this occlusion was predictable since in each trial the movement of the stimulus was occluded by a set amount and location, thus participants may have had an anticipatory response to this type of occlusion. Using random occurrences of partial occlusion during the presentation of a unimodal stimulus would reduce this predictability and reflect a more real life situation. The use of random occlusion could also be extremely effective in terms of understanding multisensory integration in terms of responding to unpredictable changes in the environment. Perturbations to a stimulus are often used in the finger tapping literature to assess how synchronization is maintained through error correction (Repp and Su 2013). The use of this paradigm is particularly effective for assessing how the integration of sensory information changes, based on the reliability of the modalities. Typically, two modalities are presented in a multisensory condition and one is randomly perturbed in order to reduce its reliability (Wing et al. 2010; Elliott et al. 2010). These studies have shown that, with this paradigm, sensory weighting shifts towards the more reliable of the two modalities (i.e. the non-perturbed stimulus), in line with predictions from the MLE model. But, they are limited since only discrete stimuli with a finger tapping task have been used. Understanding how continuous movements maintain coordination with continuous stimuli is also an important question that needs to be addressed. The use of random occlusion could be an effective way of mimicking the perturbations used in the finger tapping studies and addressing this question. Importantly, this paradigm would also allow researchers to test whether the predication of the MLE model regarding sensory integration can be extended to include continuous based tasks and stimuli.

6.3.4 Saliency issues with frequency-modulated tones

The saliency of a given stimulus can greatly affect the coordination dynamics. With auditory stimuli that are presented as frequency-modulated tones, there exists a bias towards the high pitch. In study 2, this pitch bias caused better synchronization performance with the high pitch compared to the low pitch for one of the auditory conditions (AP). This pitch bias may have also affected the ability of this modality to be integrated with the visual stimuli and raises questions relating to the saliency of this type of auditory stimulus. Thus, the use of a more salient type of auditory stimulus in future work may be required. Indeed, Rodger & Craig (2011) used a very salient auditory stimulus that had no pitch bias since their stimulus was an increasing pitch of a sine tone for both the left and right directions. Comparisons between this type of salient stimulus and the frequency-modulated tones used in study 3 may be needed in order to establish whether the former stimulus can actually improve synchronization by removing the pitch bias. More generally there appears to be a lack of clarity in terms of understanding what is the most salient auditory stimulus, opening the door for future studies to address this issue.

6.3.5 The role of task difficulty in multisensory integration

The use of multisensory stimuli generally improves synchronization when compared to unimodal stimuli but the level of difficulty in the task may mediate the benefit of multisensory integration. The bimodal results, from study 2, suggested only a limited multisensory enhancement in one of the four conditions and this may have been due to the low level of task difficulty coupled with the high saliency of the visual stimulus. In study 3, there was some evidence that for specific conditions, task difficulty may have been a factor in the integration of sensory information. However, the use of occlusion is not the most effective way of adjusting the task difficulty. Increasing the frequency of the movement to be performed or reducing the saliency of the stimuli could be two ways to test the potential impact of task difficulty on multisensory integration.

Weak (i.e. poor saliency) sensory cues are known to provide significant enhancement when presented together in contrast to strong (i.e. good saliency) sensory cues (Ernst and Bülthoff 2004). Thus, using less salient sensory cues in a synchronization task may be a useful way of adjusting the task difficulty while at the same time assessing whether or not the saliency of the stimuli affects sensory integration (Varlet et al., 2012). A similar approach has been made in the perception literature. Alais & Burr (2004) presented participants with an audio-visual stimulus but reduced the saliency of the visual element by blurring the visual dot by various amounts in order to see how this would affect the sensory weighting of each of these modalities when integrated. Instead of only adjusting one modality, it would be advantageous to adjust the saliency of both modalities in order to assess whether low saliency of the stimuli improves the level of sensory integration due to an increase in task difficulty. This could be achieved with an auditory modality by reducing the volume by different amounts or by adding white noise in the background. With the visual modality reducing the saliency could be achieved by only presenting the outline of the square or adjusting the colour of the square so that it becomes closer to the background colour. Combining these two modalities with reduced saliency in a synchronization task would allow for an assessment of whether saliency mediates the sensory integration by increasing the task difficulty.

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