Informational constraints on spontaneous visuomotor entrainment

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Abstract

Past research has revealed that an individual’s rhythmic limb movements become spontaneously entrained to an environmental rhythm if visual information about the rhythm is available and its frequency is near that of the individual’s movements. Research has also demonstrated that if the eyes track an environmental stimulus, the spontaneous entrainment to the rhythm is strengthened. One hypothesis explaining this enhancement of spontaneous entrainment is that the limb movements and eye movements are linked through a neuromuscular coupling or synergy. Another is that eye-tracking facilitates the pick up of important coordinating information. Experiment 1 investigated the first hypothesis by evaluating whether any rhythmic movement of the eyes would facilitate spontaneous entrainment. Experiments 2 and 3 (respectively) explored whether eye-tracking strengthens spontaneous entrainment by allowing the pickup of trajectory direction change information or allowing an increase in the amount of information to be picked-up. Results suggest that the eye-tracking enhancement of spontaneous entrainment is a consequence of increasing the amount of information available to be picked-up.

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1. Introduction

The movements of people are often entrained to external or environmental visual rhythms. Such coordination occurs for example when juggling with three or more balls, when the hands of a juggler become coordinated in time and space with the movements of the balls (Beek, 1989; Beek & Turvey, 1992). The movements of an individual are also often coordinated to the rhythmic movements produced by other people (Schmidt & Richardson, 2008). The postural or limb movements of two or more people tend to spontaneously synchronize when talking, walking or acting together for instance (Néda, Ravasz, Brechet, Vicsek, & Barabási, 2000; Ramenzi, Davis, Riley, Shockley, & Baker, 2011; Schmidt & O’Brien, 1997; Shockley, Santana, & Fowler, 2003; Tognoli, Lagarde, DeGuzman, & Kelso, 2007; van Ulzen, Lamoth, Daffertshofer, Semin, & Beek, 2008; Varlet, Marin, Lagarde, & Bardy, 2011). Such interpersonal visuomotor coordination has received a growing amount of attention from researchers because there is evidence that it modulates the success of everyday social interactions (Marsh, Richardson, & Schmidt, 2009; Wiltermuth & Heath, 2009). Coordinated movements in a dyad or group of people can enhance for example feelings such as social connectedness, affiliation and even the efficiency of their communication (Bernieri, 1988; Chartrand & Bargh, 1999; Hove & Risen, 2009; Miles, Lumsden, Richardson, & Macrae, 2011; Richardson, Dale, & Kirkham, 2007; Shockley, Richardson, & Dale, 2009; Wiltermuth & Heath, 2009).

Previous research has found that the dynamics of visuomotor coordination is modulated by how the actor visually attends to the movements of the external or environmental stimulus (Huys & Beek, 2002; Richardson, Marsh, Isenhower, Goodman, & Schmidt, 2007; Roerdink, Bank, Peper, & Beek, 2013; Roerdink, Ophoff, Peper, & Beek, 2008; Roerdink, Peper, & Beek, 2005; Schmidt, Richardson,Arsenault, & Galantucci, 2007). In particular, it has been shown that the occurrence of spontaneous visuomotor entrainment depends on whether or not the actor visually tracked the movements of the stimulus with the eyes (Romero, Coey, Schmidt, & Richardson, 2012; Schmidt et al., 2007; Varlet, Coey, Schmidt, & Richardson, 2012a). Specifically, tracking a stimulus with the eyes has been found to enhance entrainment. The origin of this effect, however, remains largely unknown. Here we present three experiments that were aimed at gaining a better understanding of the influence of eye movements on the occurrence of spontaneous visuomotor entrainment.

Numerous studies have demonstrated that the dynamics of rhythmic visuomotor coordination can be understood as constrained by the dynamical entrainment processes of interacting oscillators (Byblow, Chua, & Goodman, 1995; Coey, Varlet, Schmidt, & Richardson, 2011; de Rugy, Oullier, & Temprado, 2008; Peper & Beek, 1998; Richardson et al., 2007; Schmidt, Carello, & Turvey, 1990; Schmidt & O’Brien, 1997; Snapp-Childs, Wilson, & Bingham, 2011; Tognoli et al., 2007; Wimmers, Beek, & van Wieringen, 1992). These processes have been found to underlie the organization and stability of a wide range of oscillatory systems involving a variety of components (Pikovsky, Rosenblum, & Kurths, 2001; Strogatz, 2003). This includes for instance the emergence of coordinated behavior in groups of planets, neurons or humans. Previous studies that investigated rhythmic bimanual coordination provided the first evidence of dynamical entrainment processes in human movement systems (Haken, Kelso, & Bunz, 1985; Kelso, 1984, 1995; Schöner, Haken, & Kelso, 1986). Coupled by neuromuscular information, the movements of two hands of an individual become spontaneously synchronized (Kelso, Southard, & Goodman, 1979). Such synchronization occurs in one of two possible modes: an in-phase pattern of coordination where the hands move at the same time in the same direction or an anti-phase pattern of coordination where the hands move at the same time in opposite direction (Kelso, 1984, 1995). In addition, previous research has shown that anti-phase coordination is less stable than in-phase coordination as indicated by greater variability and can only be maintained for slow to moderate movement frequencies (Kelso, 1984, 1995). Typical of coupled oscillators systems, the occurrence and stability of rhythmic bimanual coordination has also been found to depend on the difference between the preferred or natural movement frequencies of each hand (Fuchs, Jirs, Haken, & Kelso, 1996; Sternad, Turvey, & Schmidt, 1992). This effect has been largely illustrated in previous research using a wrist pendulum paradigm (Schmidt, Shaw, & Turvey, 1993; Sternad et al., 1992; Treffner & Turvey, 1995). In these studies, participants are instructed to swing and coordinate hand-held pendulums about the wrist that either have the same or different natural frequencies (manipulated by changing
the position of the mass attached). The results demonstrate that the most stable coordination occurs when participants are instructed to coordinate identical pendulums (Schmidt et al., 1993; Sternad et al., 1992; Treffner & Turvey, 1995). Furthermore, the stability of the coordination progressively decreased, the greater the difference between the pendulums’ natural frequencies.

Of particular relevance for the current study is that such dynamical entrainment processes have not only been found between the limb movements of a single individual (i.e., intrapersonal coordination), but also between the limb movements of an individual and external visual rhythms, including the rhythmic movements produced by other people (i.e., interpersonal coordination) (Issartel, Marin, & Cadopi, 2007; Lopresti-Goodman, Richardson, Silva, & Schmidt, 2008; Peper & Beek, 1998; Schmidt & O’Brien, 1997; Tognoli et al., 2007; van Ulzen et al., 2008; Varlet et al., 2012a; Wimmers et al., 1992). That is, when an individual is visually coupled to a stimulus movement or rhythm, the movements of the individual can become spontaneously synchronized toward an in-phase or anti-phase pattern of coordination. As with interpersonal interlimb coordination, in-phase is more stable than anti-phase and tends to be observed more often. Moreover, the stability of such visuomotor coordination is similarly modulated by the difference between preferred movement frequencies of the actor and the observed stimulus rhythm (Lopresti-Goodman et al., 2008; Richardson, Marsh, & Schmidt, 2005; Schmidt & O’Brien, 1997).

Visuomotor coordination, however, is typically weaker and less stable than intrapersonal coordination (i.e., coordination between or within limbs’ movements of an individual) (Richardson, Lopresti-Goodman, Mancini, Kay, & Schmidt, 2008; Schmidt, Bienvenu, Fitzpatrick, & Amazeen, 1998). The decreased stability of visuomotor coordination is due in part to the nature of the visual coupling, which is weaker than the neuromuscular coupling that characterizes intrapersonal interlimb coordination. The movement intention of the actor when viewing stimulus rhythm also plays a significant role in shaping the stability and intermittency of visuomotor coordination. Although still more variable than intrapersonal interlimb coordination, when an actor intends to coordinate with a visual rhythm the coordination can be maintained absolutely, in that movements of the actor become phase locked with the visual rhythm in either an in-phase and anti-phase pattern over time. When an actor has no specific intention to coordinate with an observed stimulus rhythm, coordination can still occur, however tends to be relative (instead of absolute) or intermittent (von Holst, 1973) with the actor spontaneously falling in and out of coordination over time. For such unintentional or spontaneous coordination the difference between the participant preferred movement frequency and stimulus frequency has to be small enough to be compensated by a weak visual coupling (Lopresti-Goodman et al., 2008). Otherwise, the limb of the participant moves in time and space totally independent of the stimulus’ movements and no spontaneous entrainment or coordination appears. However, there is evidence that the strength of such a visual coupling is mediated by the degree to which an actor attends to the displacements of the external or environmental rhythm (Richardson et al., 2007; Schmidt et al., 2007).

More specifically, previous research has shown that the stability of the coordination depends on whether the actor visually tracked stimulus displacements with eye movements (Romero et al., 2012; Schmidt et al., 2007; Varlet et al., 2012a). Schmidt et al. (2007) investigated the spontaneous entrainment between the pendulum swinging of participants and a visual stimulus that oscillated horizontally on a projection screen. Participants were instructed to oscillate their pendulum at their preferred tempo and maintain this tempo while reading letters that were displayed at random intervals on the screen. The letters occurred either just above the middle of the trajectory of the oscillating visual stimulus (i.e., non-tracking condition) or on the oscillating stimulus itself (tracking condition). Although participants were only instructed to maintain their preferred tempo, the results demonstrated that their movements became spontaneously and intermittently synchronized with the stimulus movements in both the tracking and non-tracking conditions. More importantly, the results revealed that synchronization was stronger in the tracking condition (i.e., when participants tracked the stimulus displacements with their eyes) as indicated by more occurrence of in-phase or anti-phase coordination.

Although these results have been replicated in other studies (Romero et al., 2012; Varlet et al., 2012a), the origin of this constructive eye-tacking effect on spontaneous visuomotor entrainment is still an open question. Specifically, why does tracking a stimulus movement with the eyes
increase the occurrence of spontaneous visuomotor entrainment? A possible explanation is that the movements of the eyes establish an intrapersonal eye–limb neuromuscular coupling or synergy that when added to the visual coupling increases the entrainment. Numerous studies have found mutual influences between eye and limbs’ movements and support the existence of such a neuromuscular coupling (Engel, Anderson, & Soechting, 2000; Falciati, Gianesini, & Maioli, 2013; Gauthier, Vercher, Ivaldi, & Marchetti, 1988; Koken & Erkelens, 1992; Lünenburger, Kutz, & Hoffmann, 2000; Maioli, Falciati, & Gianesini, 2007; van Donkelaar, Lee, & Drew, 2000). First, there is evidence that the movements of a limb can influence the dynamics of eye movements. Saccadic eye movements are faster when they are accompanied by arm movements, for instance (Lünenburger et al., 2000; Snyder, Calton, Dickinson, & Lawrence, 2002). The movements of a limb also modulate the dynamics of smooth pursuit eye movements. For example, the efficiency of smooth visual pursuit can be enhanced when an actor also tracks the moving target with his or her arm (Gauthier, Vercher, Ivaldi, & Marchetti, 1988; Koken & Erkelens, 1992; Leist, Freund, & Cohen, 1987; van Donkelaar & Lee, 1997). Previous research has shown for example that saccadic eye movements can increase the accuracy of limb movements when performed simultaneously (Abrams, Meyer, & Kornblum, 1990). The execution of arm movements has been found to be faster when accompanied by saccade eye movements (Gueugneau, Crognier, & Papaxanthis, 2008). The limbs movements of an individual are also influenced by smooth pursuit eye movements (Hiraoka, Kurata, Sakaguchi, Nonaka, & Matsumoto, 2013; Maioli et al., 2007). Maioli et al. (2007), for example, has demonstrated changes in corticospinal excitability of arm and hand muscles during smooth pursuit eye movements. Together, these results provide evidence of a synergistic relation between eye and limb movements and support the assumption that enhancement of visuomotor entrainment with eye tracking might originate from an intrapersonal eye–limb neuromuscular coupling.

Another possibility for the constructive effects of visual tracking on visuomotor synchronization is that visual tracking increases the ability of an actor to detect the kinematic information that best supports such coordination. Previous studies on intentional visuomotor coordination have demonstrated that certain locations of the movement trajectory of an oscillating visual stimulus contain particularly pertinent movement information for stable coordination making it possible for visual tracking to facilitate the pick up of this information. In particular, this research has shown that when an actor intentionally coordinates the movements of a limb with a stimulus oscillating horizontally, he or she tends to preferentially pick up information about stimulus displacements by gazing at the endpoints of its trajectory (Roerdink et al., 2005). Such gaze behaviors principally occur for stimuli oscillating at fast frequencies — when eye-tracking, and thus the pick up of the entire stimulus trajectory, become inefficient due to physiological limitations of smooth pursuit eye movements (Roerdink et al., 2005). Consistent with these findings, other research has shown that fixations on the turn-around points of the stimulus trajectory result in participants’ movements being locally more anchored in time and space, which favors stable coordination (Beek, 1989; Byblow, Carson, & Goodman, 1994; Fink, Foo, Jirsa, & Kelso, 2000; Roerdink et al., 2005, 2008, 2013). Also confirming the importance of the turn-around points of the stimulus trajectory is previous research that occluded different locations of the movement trajectory of an oscillating stimulus when participants performed an intended in-phase or anti-phase coordination (Hajnal, Richardson, Harrison, & Schmidt, 2009; Huys, Williams, & Beek, 2005). Results revealed that the least stable coordination occurred when the turn-around points or endpoints of the stimulus trajectory were occluded, which further demonstrates that they are the privileged parts of the trajectory providing critical movement information. The importance of the turn-around points of oscillating stimuli might be explained by the slowness of this part of the trajectory, which would facilitate the detection of critical movement information (Bingham, 2004; Bingham, Zaal, Shull, & Collins, 2001; Hajnal et al., 2009; Wilson, Collins, & Bingham, 2005; Zaal, Bingham, & Schmidt, 2000). Supporting this latter assumption is recent study that investigated visuomotor coordination with different stimulus velocity profiles,
which demonstrated that greater slowdown to the endpoints of the stimulus trajectory enhanced entrainment (Varlet et al., 2014).

The past research outlined above, therefore, suggests two hypotheses for why eye tracking increases spontaneous or unintentional visuomotor entrainment. One hypothesis is that the limb movements entrain to the moving eyes through a neuromuscular coupling or synergy linking the eyes and limb and when added to visual coupling reinforces the entrainment. Another hypothesis is that entrainment is strengthened because eye tracking allows for the pick up of important movement information at the endpoints or turn-around points of the movement trajectory of the stimulus. The following three experiments were aimed at investigating these two hypotheses.

2. Experiment 1

The current experiment investigated whether the eye-tracking enhancement of spontaneous visuo-motor entrainment is due to a neuromuscular eye–limb coupling in which the movement of the eyes entrains the movement of the limbs. This hypothesis predicts that any rhythmic movement of the eyes at the same tempo of a stimulus should be sufficient to enhance the occurrence and magnitude of spontaneous entrainment between an individual’s rhythmic limb movements and an oscillating visual stimulus. Consequently, in Experiment 1, participants were instructed to swing a wrist-pendulum while rhythmically moving their eyes horizontally or vertically to test whether both kinds of eye movements enhanced spontaneous visuomotor entrainment.

2.1. Method

2.1.1. Participants

Thirty undergraduate students from the College of the Holy Cross volunteered to participate in this study either for a small stipend or partial course credit. One participant was eliminated from the data set in the horizontal condition because he/she was not moving his or her wrist at a consistent tempo throughout the trials. All participants had normal or corrected-to-normal vision. The experiment was approved by the College of the Holy Cross Institutional Review Board.

Fig. 1. Illustration of the experimental setup.
2.1.2. Materials

Participants sat in a chair positioned parallel to a 40-inch high-definition television screen (Sony KDL-40XBR4). The chair had a forearm support parallel to the ground on the right-hand side and a chin rest platform that assured that the participant’s head remained stationary (see Fig. 1). The chair was positioned 0.6 m from the screen so that when the participant’s head was turned sideways toward the screen and his or her chin rested on the chin rest, the participant’s center of gaze was in line with the center of the projection screen. A hand-held pendulum was constructed from a wooden dowel 60 cm long with a 200-g plastic weight attached to its base. The participants swung the pendulum in the sagittal plane using ulnar–radial deviation of the wrist joint. These movements were recorded at a sample rate of 100 Hz using an electrogoniometer (Biometrics Ltd., Ladysmith, VA) attached on the back of the hand (under the middle knuckle) and 12–15 cm up the forearm. A PC computer was programmed to record the wrist oscillation time series as well as to create the oscillation of a visual stimulus on the projection screen and display the letters that participants had to read.

2.1.3. Procedure

Participants were told that the study was investigating multitask performance and the effect of a distraction (i.e., pendulum swinging and oscillating stimulus on the screen) on a reaction time task (i.e., reading the letters as quickly as possible). What was really being studied was the spontaneous entrainment of the participant’s wrist movements to the stimulus oscillating and the visual information that was the basis for that entrainment. Participants were told that their primary task consisted of reading aloud as quickly as possible letters that appeared on the screen, whereas their secondary task was the swinging of a handheld pendulum. The participants were instructed to swing their pendulum at a comfortable tempo (i.e., “one they could do all day”) with their forearm supported. These instructions ensured that any entrainment between the wrist and oscillating stimulus exhibited would be unintentional.

Each experimental session consisted of twenty-three 40 s trials that involved the three kinds of eye-tracking conditions—control, eye-stationary, and eye-movement (either horizontal or vertical). In the control condition, participants read letters that appeared on a stationary stimulus in the middle of the screen. Although no horizontally oscillating stimulus was present, the computer program generated an oscillating stimulus time series. The coordination in these control trials between the invisible stimulus time series and the movement of participants was used to assess chance-level coordination. In the eye-stationary condition, the letters to be read appeared on a stationary square in the middle of the screen just below the center of the trajectory of the horizontally oscillating stimulus (thus requiring no eye-movements). In the horizontal eye-movement condition, the letters appeared on squares placed 1 cm beyond the end of the horizontally oscillating stimulus endpoints (49 cm apart corresponding to 24° angular deviation). In the vertical eye-movement condition, the letters appeared on squares above and below (i.e., perpendicular to) the center of the trajectory of the horizontally oscillating stimulus (37.5 cm apart corresponding to 18° angular deviation). Letters appeared on these squares at the rhythm of the horizontally oscillating stimulus thus ensuring that the participant was making horizontal or vertical eye movements at a tempo of the oscillating stimulus (see Fig. 2). It should be noted that the movements being made by the eyes are different from those made in previous investigations (e.g., Schmidt et al., 2007) in that they are not pursuit movements of an oscillating stimulus but rather rhythmic, open-loop movements between two targets. In all conditions, asterisks appeared in addition to the letters to discourage the participants from rhythmically speaking as well as rhythmically moving their wrists. Participants were told to ignore the intermittent asterisks and say just the names of the letters that appeared as accurately and quickly as possible.

Five initial trials were used to measure each participant’s preferred, comfort mode period of oscillating the pendulum. During these trials, participants read letters that appeared on a stationary square while finding a comfortable tempo to swing the pendulum (similar to the control condition). The three most consistent trials containing the lowest variability were then averaged to estimate the participant’s comfort mode period and used as the basis for determining the period of the oscillating stimulus for the experimental trials. The three stimulus frequency conditions used were the comfort mode frequency, the comfort mode frequency – 5% (slightly slower) and the comfort mode frequency + 5% (slightly faster). The 18 experimental trials consisted of two block randomizations of the experiment’s
nine within-subjects conditions—eye tracking (control, movement and stationary) × stimulus frequency (slower, comfort, faster). Note that participants performed only in the vertical or horizontal eye movement conditions (i.e., eye movement direction was a between-subjects variable). Participants were reminded throughout the experiment to try to maintain their comfort tempo for the entirety of the experiment and to say the letters as quickly as possible. After completing all 23 trials, participants were debriefed and thanked for their participation.

2.2. Results and discussion

To evaluate the strength and patterning of the spontaneous synchronization that emerged, the distribution of relative phase angles formed between the wrist and the oscillating stimulus across the conditions was assessed. Relative phase time series between -180° and 180° were calculated, and the frequency of occurrence of these absolute relative phase angles across nine 20° regions of relative phase between 0° and 180° was determined (Richardson et al., 2005; Schmidt & O’Brien, 1997). Spontaneous entrainment is indicated by a concentration of relative phase angles in the areas of the distribution near 0° and 180° (Schmidt et al., 2007). These data were analyzed using a 2 × 3 × 3 × 9 analysis of variance with a between-subjects variable of eye movement direction (14 participants in horizontal and 15 participants in vertical) and within-subjects variables of eye-tracking (control, movement and stationary), stimulus frequency (slower, comfort, faster) and phase region (0–20°, 21–40°, …, 161–180°). Adjustments for violations of sphericity were made as necessary.

In addition to a main effect of phase region, $F(1.8, 48.8) = 5.48, p = .007, \eta^2_p = .18$, the analysis revealed significant interactions of phase region by eye tracking, $F(5.4, 146) = 3.430, p = .005, \eta^2_p = .11$, and phase region by frequency, $F(4.8, 129.49) = 2.78, p = .02, \eta^2_p = .09$. These effects replicate
past results and indicate, respectively, more in-phase spontaneous entrainment when the eyes moved with the stimulus and when the stimulus tempo was either at the comfort tempo or slightly faster (Schmidt et al., 2007).

Guided by a marginally significant interaction between phase region, eye-tracking and eye movement direction, $F(5.4, 146) = 1.91, p = .09, \eta^2_p = .07$, planned follow-up $3 \times 3 \times 9$ repeated measures ANOVAs with factors of eye-tracking, stimulus frequency and phase region were performed for the horizontal and vertical eye movement direction groups. The analysis for the horizontal movement direction (Fig. 3, top) yielded a significant interaction between phase region and eye tracking, $F(4.2, 55.12) = 4.11, p = .005, \eta^2_p = .24$, revealing significantly more spontaneous entrainment in the in-phase 0–20° region when the eyes moved horizontally compared to the no eye movement condition and the control condition (both $p < .05$). Moreover, further replicating past results, the no eye movement condition also yielded some, though a lesser, spontaneous entrainment as demonstrated by a significantly greater than chance (control condition) relative phase occurrence in the 21–40° in-phase region ($p < .05$). Alternatively, the analysis of the vertical movement direction data yielded no significant interaction between region by tracking but only a main effect of phase region, $F(2.05, 28.74) = 5.20, p = .01, \eta^2_p = .27$. As seen in Fig. 3(bottom), the (vertical) eye movement condition

![Fig. 3. Relative phase distributions obtained for each eye-tracking condition in Experiment 1. The results obtained for the groups that performed horizontal and vertical eye movements are represented at the top and bottom of the figure, respectively.](image-url)
yielded no more in-phase entrainment than either the no eye movement condition or the chance control condition.

In summary, vertical rhythmic eye movements did not increase the spontaneous entrainment of the swinging of the wrist pendulum with the horizontally moving stimulus whereas horizontal eye movements, in spite of the fact that they were targeting rather than pursuit movements, augmented the spontaneous entrainment observed. Hence, it does not seem that any rhythmic eye movements at the tempo of a stimulus enhances spontaneous entrainment to the stimulus. A neuromuscular coupling or synergy hypothesis for such eye-tracking facilitation would predict such an assimilation of the limb rhythm by the eye rhythm by virtue of neuromuscular linkages. Consequently, it does not seem that a strong form of the neuromuscular coupling or synergy hypothesis is supported by the data. Although the results do not rule out the possibility of such neuromuscular synergy exists exclusively when the eye movements and the limb movements are in the same plane, they provide support for the possibility that tracking a stimulus with one’s eye's increases spontaneous entrainment because it facilitates the pick up of important movement information. Eye movements may allow one to pick-up (i) a better quality or/and (ii) a greater amount of information about the rhythmic stimulus, and hence, increase the spontaneous entrainment to the environmental rhythm. These two possibilities are investigated in the next two experiments.

3. Experiment 2

One explanation for the eye-tracking enhancement of spontaneous visuomotor entrainment is that eye tracking allows information about the trajectory endpoints, which contains important direction-change information, to be picked, hence, enhancing coordination. As explained in the introduction, evidence supporting the importance of trajectory endpoints or turn-around points comes from a number of different studies. Hajnal et al. (2009) occluded different parts of the trajectory of an oscillating stimulus during intended visuomotor coordination and found less stable coordination when the trajectory endpoints were occluded. Roerdink et al. (2005) demonstrated that participants when coordinating with an oscillating stimulus preferentially pick up information by gazing at the endpoints of the trajectory. The authors argued that such fixation on the endpoints of an oscillating trajectory result in movements being more anchored in time and space helping to create stable coordination (Beek, 1989; Byblow et al., 1994; Huys et al., 2005; Roerdink et al., 2008). Consequently, eye-tracking’s enhancement of spontaneous entrainment may result from its allowing trajectory endpoint information to be more effectively picked up. Experiment 2 investigated the importance of this direction change information for spontaneous visuomotor entrainment.

3.1. Methods

3.1.1. Participants

Thirty undergraduate students from the College of the Holy Cross volunteered to participate in this study. Three participants were eliminated from the dataset in the center fixation condition because they did not perform the task correctly; their data demonstrated close to perfect coherence, indicating that they intentionally entrained to the stimulus. All participants had normal or corrected-to-normal vision. The experiment was approved by the College of the Holy Cross Institutional Review Board.

3.1.2. Materials

The materials used for Experiment 2 were the same as Experiment 1 except that the hand-held pendulum was constructed from a wooden dowel 50 cm rather than 60 cm.

3.1.3. Procedure

The participants’ task was the same as in the Experiment 1: participants read aloud as quickly as possible letters that appeared on the screen, while simultaneously swinging a handheld pendulum at a preferred comfort tempo. Moreover, each participant again performed this task in three different eye-tracking conditions: control, eye-movement and eye-stationary. The control condition (used to
evaluate chance entrainment) was identical to Experiment 1. The eye-movement condition was a visual tracking condition in which the letters appeared in a 2 cm square that oscillated horizontally on the screen (49 cm apart corresponding to 24° angular deviation) requiring pursuit eye-movements. Different in this experiment were the eye-stationary conditions. In these, the letters appeared on a stationary square that was placed in one of three locations, either under the center, right side or left side of the trajectory of the horizontally oscillating stimulus. These eye-stationary configurations created conditions in which the participants were forced to focus on either the middle, the right end point or the left end point of the oscillating square trajectory. Each participant performed in only one of the three no eye-movement conditions and this defined the variable of non-tracking stimulus placement as a between-subjects variable. In all conditions, the letters to be read appeared randomly at time intervals between 0 and 2 s either on the oscillating square (for the eye-movement conditions) or on a stationary square (for the no eye-movement conditions and control condition). As in Experiment 1, the frequency of the oscillating stimulus was manipulated to create three conditions, the comfort mode frequency, the comfort mode frequency – 5% (slightly slower) and the comfort mode frequency + 5% (slightly faster). Again, five initial trials were used to measure each participant’s preferred, comfort mode period of oscillating the pendulum. Each session was also comprised of 18 experimental trials that were 40 s long and consisted of two block randomizations of the nine within-subjects conditions — eye tracking (control, eye-movement and no eye-movement fixation) x stimulus frequency (slower, comfort and faster).

3.2. Results and discussion

To compare the kind and degree of spontaneous synchronization that emerged to that in previous studies which had just used the center non-tracking condition, the distribution of relative phase angles between the wrist and the oscillating stimulus for just the center non-tracking data was analyzed using a 3 x 3 x 9 repeated-measures ANOVA with variables of eye tracking (control, eye-movement and center eye-stationary fixation), stimulus frequency (slower, comfort and faster) and phase region (0–20°, 21–40°, …, 161–180°). Adjustments for violations of sphericity were made as necessary. The analysis replicated past results (e.g., Schmidt et al., 2007) by demonstrating that greater than chance spontaneous entrainment occurred for both the tracking and non-tracking conditions (Tracking Region: $F(16, 144) = 4.53, p < .001, \eta^2_p = .34$) with a trend for entrainment being greater for tracking compared to non-tracking near anti-phase. This verifies that the center non-tracking data are consistent with what has previously been observed.

To determine whether location of the stimulus affected the strength of the non-tracking entrainment, in particular, whether locating the non-tracking stimulus near the endpoints of the cycle would increase spontaneous entrainment, a mixed 3 x 3 x 9 ANOVA with a between-subjects variable of non-tracking stimulus placement (center, left and right) and within-subjects variables of stimulus frequency (slower, comfort, faster) and phase region (0–20°, 20–40°, …, 160–180°) was performed on the relative phase of the non-tracking trials. It revealed a significant interaction of non-tracking placement and phase region ($F(16, 216) = 2.63, p < .001, \eta^2_p = .16$) with the center placement condition exhibiting greater in-phase entrainment than placement on either the right or the left ends of trajectory (Fig. 4). This result is counter to expectations that direction change information available at the left or right ends of trajectory would strengthen spontaneous entrainment and argues against the claim that eye tracking of a stimulus promotes greater entrainment because it allows more direction change information to be picked up.

It still remains possible, however, that eye movements strengthen spontaneous entrainment by virtue of allowing more information about the stimulus to be picked up. The superiority of the center placement of the non-tracking stimulus over right and left placement supports this possibility because kinematic information to the right and left of a center focus would still be in the periphery of the visual field and more information could arguably be picked up in this center-focus condition. This assumption is also in line with a study by Richardson et al. (2007) who found stronger interpersonal entrainment between two individuals’ movements when they looked at each other using the focal rather than the peripheral vision, a condition that might have allowed the pick up of more movement information. Experiment 3 investigated the hypothesis of whether increasing the amount of
information to be picked up would increase spontaneous entrainment while simultaneously controlling for eye movements.

4. Experiment 3

Although the previous experiment discounts the possibility that eye-tracking enhances spontaneous entrainment because it allows coordination relevant information at the turn-around points of the trajectory to be picked-up, the possibility remains that eye-tracking enhances spontaneous entrainment because it allows a greater amount of information to be picked-up. Accordingly, this last experiment manipulated the amount of information available about a rhythmic stimulus while controlling eye movements to see whether spontaneous entrainment is enhanced when more information is available. The amount of information available was controlled by varying whether the rhythmic stimulus was in focal or peripheral view.

4.1. Methods

4.1.1. Participants

Thirty students from the College of the Holy Cross volunteered to participate in this study for either a small stipend or partial course credit. All participants had normal or corrected-to-normal vision. The experiment was approved by the College of the Holy Cross Institutional Review Board.

4.1.2. Materials

The same materials used in the previous experiments were used in this experiment. However, the computer generated rhythmic stimulus was not a square that oscillated horizontally but a square that expanded and contracted rhythmically in size so that it appeared to move forward and backward in depth. Consequently, the participants’ chair was placed facing the screen rather than parallel to it. Additionally, the participants were no longer required to place their chins in the chin rest.

4.1.3. Procedure

The participant’s task was the same as in the previous experiments: To read letters that appeared on the screen aloud as quickly as possible while swinging a handheld pendulum at a preferred comfort tempo. However in this experiment, the participants performed this task in three conditions in which the eyes were always stationary. The control condition was the same as in the previous experiments (i.e., no rhythmic stimulus and letters appeared on a stationary stimulus in the middle of the screen)
but the two other conditions differed. In the focal fixation condition, letters appeared in the center of the expanding and contracting stimulus. In the non-focal fixation condition, letters appeared on a stationary square directly below the expanding and contracting stimulus. These displays created conditions in which the participants were either visually focusing directly on the rhythmically moving stimulus (focal fixation) or not (non-focal fixation) while at the same time keeping their eyes stationary. As in the previous experiments, the frequency of the rhythmic stimulus was manipulated in three conditions, the comfort mode frequency, the comfort mode frequency $- 5\%$ (slightly slower) and the comfort mode frequency $+ 5\%$ (slightly faster). The 18 experimental trials were 40 s long and consisted of two block randomizations of the experiment's nine within-subjects conditions—perceptual focus (control, focal fixation and non-focal fixation) $\times$ stimulus frequency (slower, comfort and faster).

4.2. Results and discussion

The distribution of relative phase angles between the wrist and the oscillating stimulus were analyzed using a $3 \times 3 \times 9$ analysis of variance with within-subjects variables of perceptual focus (control, focal fixation and non-focal fixation), frequency (slower, comfort, faster) and phase region ($0–20^\circ$, $21–40^\circ$, …, $161–180^\circ$). Note that in-phase ($0^\circ$) coordination was defined as the pendulum moving towards the display as the rhythmic stimulus was getting smaller while anti-phase ($180^\circ$) coordination was defined as the pendulum moving towards the display as the rhythmic stimulus was getting larger. Adjustments for violations of sphericity were made as necessary.

The analysis revealed a significant effect of phase region, $F(2.2, 63.74) = 5.015$, $p < .001$, $\eta_p^2 = .15$, as well as an interaction between perceptual focus and phase region, $F(4.73, 137.08) = 3.678$, $p < .001$, $\eta_p^2 = .11$. No other effects were significant. As seen in Fig. 5, greater than chance spontaneous entrainment near in-phase was attained for the focal fixation condition ($p = .02$) but not the non-focal fixation condition ($p > .05$). However, greater than chance spontaneous entrainment near anti-phase was found for both the focal fixation and the non-focal fixation conditions in both the $141–160^\circ$ ($p = .03$ and .006) and $161–180^\circ$ ($p = .01$ and .007) phase regions. The results suggest that focal fixation created a stronger perceptual coupling than non-focal fixation when the pendulum moves towards the display as the rhythmic stimulus was getting smaller (in-phase) but an equally strong perceptual coupling compared to non-focal fixation when the pendulum moves towards the display as the rhythmic stimulus was getting larger (anti-phase). It is possible that the looming nature of the object getting larger when the pendulum is being moved towards the screen may automatically draw the attention of

![Fig. 5. Relative phase distributions obtained for the different perceptual focus conditions in Experiment 3.](image-url)
the perceiver toward the object because it specifies an imminent virtual collision with the perceiver's movement (Gibson, 1958; Lee, 1976). This interpretation plus the fact that the focal fixation perceptual coupling was stronger when the pendulum moves towards the display as the rhythmic stimulus was getting smaller (in-phase) seems to indicate that increasing visual attention enhances spontaneous entrainment, and hence, provides evidence that greater information pick up is the underlying reason for why visually tracking a stimulus induces greater spontaneous entrainment.

5. General discussion

Previous research has shown that the limb movements of an actor become spontaneously coordinated with the movements of external or environmental visual rhythms and that such entrainment is stronger when the actor visually tracked the movements of the stimulus with the movements of the eye. The aim of the present study was to understand why this is. Across three experiments, we addressed two possible explanations of this phenomenon. The first is that a neuromuscular coupling or synergy between the eye and limb movements plays a mediating role in entraining the limb movements to the rhythmic stimulus. The second explanation is that eye movements enhance spontaneous entrainment to the rhythmic stimulus by increasing the amount or quality of the perceptual information available.

Experiment 1 investigated the role of a neuromuscular coupling or synergy in eye movement-enhanced spontaneous entrainment by changing the direction of the eye movements being executed: The eyes produced rhythmic targeting movements in either a vertical or horizontal plane while a rhythmic stimulus oscillated in the horizontal plane. The horizontal eye movements but not the vertical eye movements enhanced spontaneous entrainment. Importantly, having the eyes move in a targeting rather than pursuit fashion did not eliminate spontaneous entrainment of the limb to the rhythmic stimulus but having the eyes move vertically rather than horizontally did. These results suggest that not any kind of rhythmic eye movement, even if they are at the same tempo of an observed stimulus, facilitates spontaneous entrainment. Of course, the horizontal targeting movements that did increase entrainment would allow for the pick up of additional information about the stimulus' kinematics that may enhance the perceptual coupling between the limb and the rhythmic stimulus, and hence, the spontaneous entrainment.

Experiment 2 investigated whether eye movements in the same plane as the horizontal stimulus allow the increased possibility of picking up sync-point information, direction change information at the turn-around points of the stimulus especially used for entraining to a rhythmic stimulus (Beek, 1989; Bingham et al., 2001; Hajnal et al., 2009; Roerdink et al., 2005, 2008). The results provided convincing evidence that the eye movement-enhanced spontaneous entrainment are not simply a consequence of the perceptual coupling being enhanced by increased direction change information: left and right side non-tracking conditions (which contained direction change information) failed to enhance spontaneous entrainment over the center non-tracking condition (which did not contain direction change information). In particular, it supports the possibility that eye movements strengthen the perceptual coupling by virtue of allowing more information about the stimulus' movement to be picked up. In other words, eye movements would enhance spontaneous entrainment to the rhythmic stimulus by increasing the amount of perceptual information available. The relative strength of center non-tracking condition over right and left non-tracking conditions (Fig. 2) supports this assumption.

Experiment 3 used a rhythmic stimulus moving in depth in which full kinematic information was available but the eyes never moved to further investigate the informational constraints on the perceptual coupling. Focal or non-focal fixations to stimulus movements were used to manipulate the amount of movement information picked-up by participants. Spontaneous entrainment was facilitated in the condition in which attentional focus, and hence presumably perceptual pick-up, was the greatest. These results demonstrate the importance of the amount of movement information picked-up for spontaneous entrainment and support the assumption that eye movements enhance entrainment by facilitating the pick up of more movement information.

Supporting the importance of the amount of movement information picked-up for the occurrence of entrainment, these results are in line with previous research that investigated informational
constraints on visuomotor coordination (Richardson et al., 2007; Roerdink et al., 2005, 2008). They corroborate the study of Richardson et al. (2007) that examined interpersonal visuomotor entrainment between the rocking chairs’ movement of two individuals and found that stronger entrainment occurred when they looked at each other using the focal rather than the peripheral vision. These results are also in line with previous studies that investigated gaze behaviors of participants during intentional visuomotor coordination (Roerdink et al., 2005, 2008). They showed that participants privileged the pick up of the endpoints of the stimulus movement trajectory but only when tracking the entire trajectory became inefficient. Indeed, as long as the stimulus oscillated below or around 1 Hz, participants preferred tracking gaze behaviors, and thus, the pick up of the entire movement trajectory of the stimulus. When the stimulus oscillated faster and visual tracking became inefficient due to physiological limitations of smooth pursuit eye movements, participants privileged fixed gaze behaviors toward the endpoints or turn-around points of the stimulus trajectory (Koken & Erkelens, 1992; Leist et al., 1987; Roerdink et al., 2005). The pick up of greater amount of movement information was privileged as much as possible to stabilize the coordination.

The results of this study also provide coherent explanations to previous research that found that eye tracking only enhanced spontaneous visuomotor entrainment with stimuli of moderate to large movement amplitudes (Varlet et al., 2012a). No advantages of eye movements have been found for stimuli oscillating horizontally with small movement amplitudes (i.e., 23° visual angle). The same degree of spontaneous entrainment or coordination occurred in tracking and non-tracking conditions. Differences at the level of the amount of movement information picked-up could explain this previous finding. For small stimulus amplitudes, the entire movement trajectory can be picked-up irrespective of eye movements. The entire movement trajectory of the stimulus is accessible even if the eyes of the actor remain fixed on the center of the stimulus trajectory. For moderate to large stimulus amplitudes, however, the entire stimulus trajectory can only be picked-up with eye tracking, which could explain the occurrence of stronger entrainment in tracking compared to non-tracking conditions.

Although our results demonstrated the importance of the amount of movement information, they do not remove the possibility that better access to turn-around points, and thus, the quality of the information picked-up, modulate as well the occurrence of spontaneous visuomotor entrainment. As explained above, the relative strength of center non-tracking over right and left non-tracking conditions supports the importance and superiority of the amount of movement information picked-up, but it remains possible that if the same amount of information could have been picked-up in all conditions, right and left non-tracking conditions would have facilitated entrainment due to better access to the turn-around points. The studies of Roerdink and his colleagues showed that the amount and the quality of the information can both modulate the stability of intentional visuomotor coordination depending on task constraints (Roerdink et al., 2005, 2008). Hajnal et al. (2009) also found that access to the endpoints modulate the stability of intentional visuomotor coordination. Although these effects might differ for spontaneous or unintentional coordination due to lower stability, it encourages further explorations in future research to examine whether access to the endpoints of the stimulus trajectory also modulates the occurrence of spontaneous visuomotor entrainment.

More generally, demonstrating the importance of eye movements in spontaneous visuomotor entrainment by facilitating the pick up of more movement information, the results of the present study open new perspectives to understand the occurrence and stability of interpersonal coordination between two or more individuals. They could provide further understanding of gaze behaviors exhibited by people during interpersonal performances such as in dance, musical or sport activities (de Brouwer, de Poel, & Hofmijster, 2013; Kawase, 2014; Phillips-Silver & Keller, 2012; Sevdalis & Keller, 2011; Travassos, Araújo, Vilar, & McGarry, 2011). They could also be of particular interest in the understanding of interpersonal coordination during everyday social interactions, and in particular, the disorders occurring with certain mental illnesses. Indeed, previous research has shown that patients suffering from schizophrenia or autism have poorer interpersonal coordination and that such movement disorders might contribute to their social interactions deficits (Fitzpatrick, Diorio, Richardson, & Schmidt, 2013; Kupper, Ramseyer, Hoffmann, Kalbermatten, & Tschacher, 2010; Marsh et al., 2013; Varlet et al., 2012b). Origins of these coordination impairments remain largely unclear, however. Our results suggest that disorders at the level of eye-tracking behaviors, and thus, at the level of the amount of information picked-up on the movements of the others, is a promising research direction to...
understand these coordination impairments. The numerous studies that have shown that these patients have abnormal eye movements support this possibility (Dalton et al., 2005; Holzman, Proctor, & Hughes, 1973; Holzman et al., 1974; Takarae, Minshew, Luna, Krisky, & Sweeney, 2004).

To conclude, the present study showed how eye tracking can modulate the occurrence of spontaneous or unintentional visuomotor entrainment. The study has confirmed the previous finding that eye tracking strengthens the spontaneous entrainment of limb’s movements of an actor with an external or environmental visual rhythm and extends it by showing that this enhancement originates from changes at the level of the perceptual coupling. The results showed that eye tracking does not strengthen entrainment due to an additional eye–limb neuromuscular coupling that would stabilize the coordination but by facilitating the pick up of more movement information. Therefore, these results further demonstrate the intrinsic link between perception and action and the necessity to examine perceptual activities to better understand coordination dynamics in motor behavior (Bingham, 2004; Gibson, 1966, 1979; Kelso, 1995; Kugler & Turvey, 1987; Mechsner, Kerzel, Knoblich, & Prinz, 2001).

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