Relationship between cardiac cycle and the timing of actions during action execution and observation.

Authors: Palser, E. R.[1,2,3]*, Glass, J.[2], Fotopoulou, A.[1], & Kilner, J. M[2].

Author Affiliations: 1 Psychology and Language Sciences, UCL, London UK 2 Sobell Department of Motor Neuroscience and Movement Neuroscience, Institute of Neurology, UCL, London UK 3 Department of Neurology, University of California San Francisco, San Francisco, USA.

*Correspondence: eleanor.palser@ucsf.edu

Abstract

Previous research suggests that there may be a relationship between the timing of motor events and phases of the cardiac cycle. However, this relationship has thus far only been researched using simple isolated movements such as key-presses in reaction-time tasks and only in a single subject acting alone. Here, we investigated how the cardiac cycle relates to ongoing self-paced movements in both action execution and observation using a novel dyadic paradigm. We recorded electrocardiography (ECG) in 26 subjects who formed 13 dyads containing an action executioner and observer as they performed a self-paced sequence of movements. We demonstrated that heartbeats are timed to movements during both action execution and observation. Specifically, movements were more likely to culminate between heartbeats than simultaneously with the heartbeat. The same pattern was observed for action observation, with the observer's heartbeats occurring off-phase with movement culmination. These findings demonstrate that there is synchronicity between an action executioner's cardiac cycle and the timing of their movements, and that the same relationship is mirrored in an observer. This suggests that interpersonal synchronicity may be caused by the mirroring of a phasic relationship between movement and the heart.

Introduction

A growing body of research, comprising physiological and psychological investigations, is consistent with the hypothesis that the central nervous system has access to cardiac information, and uses this information to guide behaviour. One such instance is the bidirectional relationship between the cardiac cycle and the timing of movement. One of the earliest observations in this vein was that walking rate and heart rate typically show a one-to-one mapping[1,2]. It was proposed that the rhythm of the heart might represent a pacemaker, guiding the timing of movement.

A large proportion of research on the impact of cardiac phases on behavior has involved the passive presentation of stimuli, and investigation of differences in how those stimuli are processed in different cardiac phases. It was initially suggested that afferent baroreceptor signalling at systole inhibits sensory perception[3,4] but findings of increased fear perception[5] and face recognition[6] suggest the picture is more complicated. Recently, it was found that subjects prefer to actively sample images during systole[7]. It is however unknown to what extent the motor component of the task impacted the observed finding.

Much of the previous physiological work on the relationship between the cardiac cycle and movement has employed simple prescribed movements within reaction-time and stop signal paradigms. Anticipatory cardiac slowing in the fore period of a reaction-time task while the subject prepares to move has been observed[8, 9]. The motor response was also found to vary depending on when in the cardiac cycle it occurred [10, 11], with faster reaction times during atrial contraction. A similar effect has recently been observed for movement inhibition, with faster responses to stop cues during systole[12]. These effects have been attributed to baroreceptors[13].

Research in the field of social neuroscience, meanwhile, has found both movement and cardiac synchronicity between interacting individuals. Early studies found that listeners to a speaker tend to move in time with rhythms of a speaker's speech[14] and mirror the postures of the speaker[15]. In other interactions, the direction of the effect is less apparent, with partners mimicking each other's postural sway[16] and linguistic forms[17]. In a recent study, groups of subjects (numbering between four and five individuals) constructed models out of Lego blocks[18]. They either worked collectively (where subjects took turns to work on one construction project) or individually (where subjects worked on their own construction projects side by side). More stable shared heart rate dynamics were observed in collective trials than individual trials, increasing across the course of collective trials[18], suggesting that convergence was tied to the social nature of the task. Indeed, heart rate entrainment has been suggested as a mechanism underlying emotional commonality in social interaction, facilitating a sense of community between individuals[19], empathy[20,21] and team performance[22,23,24,25].

Findings of inter-individual synchronicity and its influence on measures of social competence are compatible with simulation theories of action understanding, which posit that in order to understand another’s behaviour, we simulate their perceptual, motor and bodily states in ourselves[26]. Such ideas have since been formalized by hierarchical predictive models, wherein it is argued that action observation results in an observer generating an internal model of how they would perform it[27,28]. Such models are proposed to contain not only exteroceptive and proprioceptive predictions, but also interoceptive predictions about how such an action might be performed[29].

The existing literature can thus be summarized as reflecting two broadly different methodological approaches to studying the relationship between the heart and movement. The first has studied the relationship between cardiac events and evoked movements such as those elicited by paradigms designed to gauge reaction time [10,30] and response inhibition[11,12]. These studies tested discrete, single movements. The second has taken the opposite approach and analyzed cardiac and movement parameters in a number of unconstrained self-paced environments, typically within a social context[18,31]. In addition, most of the findings of movement synchronicity between individuals are based on subjective, observational techniques, although see[32] for an exception.

The current study was designed to answer the previously neglected question of whether inter-individual synchronicity and cardiac-motor timing relationships are linked, bridging the gap between the two previous approaches, by investigating cardiac-motor and inter-individual synchronicity within the same paradigm. Naturalistic actions are more likely to comprise a series of goal-directed self-paced movements than discrete, cued movements. Therefore, in the present study, we sought to investigate the bidirectional relationship between the cardiac cycle and movement during a sequence of meaningful self-paced movements. Subjects were divided into dyads and took turns to perform and observe a sequence of semi-controlled movements under experimental conditions, while ECG was recorded from both. In brief, the task required both subjects within a dyad to memorize a sequence of six movement locations and then take it in turn to replicate the sequence. In this way, subjects both executed and observed the movements. The timing of movement was recorded using touch-sensitive pads.

Firstly, we investigated whether there was any relationship between the timing of the movements made, operationalized as the endpoint of the action, and the location of this event within the cardiac cycle. The endpoint of each action corresponded to each memorized location in the movement sequence. Secondly, we tested for synchronicity between individuals in a dyad, in both cardiac cycle length and movement speed. Thirdly, we tested the prediction that any phasic relationship observed between the timing of movement events and the cardiac cycle during action observation would also be observed during action observation.

Materials and Methods

Subjects

A total of twenty-six healthy adult subjects with normal or corrected-to-normal vision were recruited. Subjects were aged between 19 and 36 years (mean = 24.92, *SD* = 4.78). Fourteen were female and 12 were male. Twenty-four subjects reported being right-handed, and two reported being left-handed. Data was collected in two stages. In the first stage, due to practical reasons, subjects performed the dyadic behavioral turn taking task with an experimenter as their partner (n = 12). In stage two, the remaining subjects were recruited in pairs and performed the task together (n = 14). For analysis, data were pooled. Ethical Approval of the experimental protocol was granted by the Ethics Committee of University College London, and the methods were carried out in accordance with the declaration of Helsinki. All subjects gave written informed consent before testing.

Materials

Subjects were seated in pairs at a table in front of a Dell laptop computer. Stimuli were presented using MATLAB (version 7.8.0, Mathworks Inc., MA, USA) with the Cogent 2000 toolbox (www.vislab.ucl.ac.uk/cogent_2000.php). Three electrodes were affixed to the abdomens of subjects as per the standard Lead II configuration, to record their ECG. On the table were four touch-sensitive pads and a marble, which the subjects used to execute a series of memorized movements.

Procedure

Once seated comfortably, the experimenter affixed three disposable or washable electrodes to each subject. They were instructed that they would view movement sequences on the screen (see Figure 1A) and would have to replicate them in turns afterwards using the marble and touch-sensitive pads in front of them. They were also instructed not to talk to or interact with their partner for the duration of the experiment. On the screen, subjects viewed an animation of a sequence of six movements (see Figure 1B). The screen showed three white circles arranged in a triangle. One circle briefly turned red before returning to white to indicate the sequence. The order of the sequence was pseudo-randomized with the only constraint being that the same circle could not appear two or more times in a row. Subjects viewed the sequence twice and were instructed to memorize it. Subjects were informed that the ECG measures their heart, but were not made aware of the purpose of the experiment or that the timing of their movements were being recorded.

On the table were four touch-sensitive pads and a marble. Three of the pads were arranged in a triangle and corresponded to the circles that appeared on the screen. The fourth pad was placed in the middle and was the home pad where the marble was to be returned to at the end of each movement sequence and from where each movement sequence commenced. On each trial both subjects in the pair had to attempt to replicate the sequence, one after the other. To do this, subjects were instructed to move the marble between the touch sensitive pads in the order they believed to be the same as in the initial video (see Figure 1C). The order of which subject executed first and which second was counter-balanced across blocks for each pair. That is, turn-taking occurred by block, where the same subject took the first turn for a whole block, and then they swapped. Subjects were instructed to make the series of movements at a speed that was comfortable to them.

For 12 subjects there were two blocks of ten trials in total. In one block one subject would go first for all ten trials, and in the other the other subject would go first for all ten trials. For the remaining 14 subjects there were four blocks of ten trials in total. In two blocks one subject would go first for all ten trials, and in the other two the other subject would go first for all ten trials. Which subject was instructed to go first was alternated, so that no subject took the first turn for more than one block in a row. ECGs were recorded throughout the duration of each block.

For 18 subjects the ECG was recorded using an Active 2 Biosemi amplifier. The ECG was recorded at 2048 Hz. For the remaining seven subjects, the ECG was recorded using a CED 1401 in Spike2 at a sampling rate of 1000 Hz. The time at which the marble was placed on the touch-sensitive pad was also recorded. The experiment lasted approximately 40 minutes. Afterwards, subjects were debriefed about the purpose of the experiment and their experience of taking part, and were given the opportunity to ask the experimenter any questions.

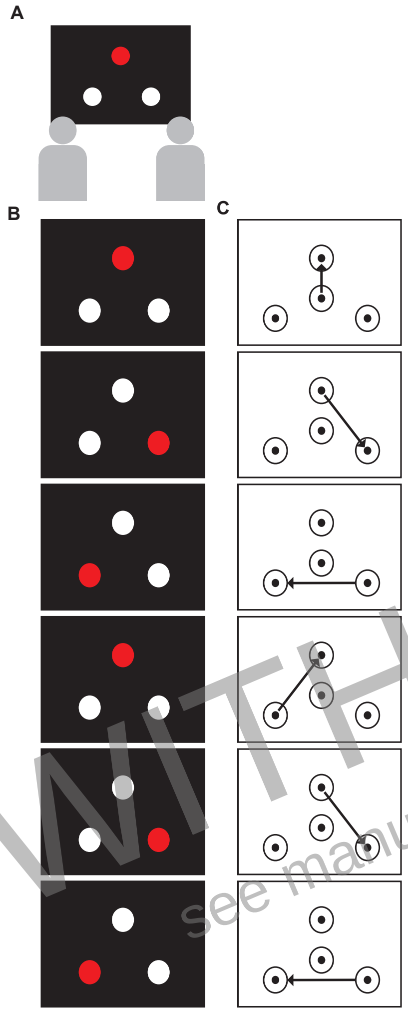

Figure 1: *Task design. Panel A: Subjects were seated side by side in front of a laptop computer; Panel B shows an example of the sequence of movements subjects were required to learn; Panel C shows how subjects would accurately replicate the sequence in (B) using the touch-sensitive containers.*

Analysis

For all subjects the three electrode ECG recordings were transformed offline by linear subtraction into two sets of bipolar recordings, which in turn were averaged to produce a single ECG recording for each subject. For all subjects, the time of the peak of the R-wave of each heartbeat was calculated from the ECG. First, the ECG data were high pass filtered at 0.01 Hz to remove any linear drift. Second, a threshold was determined from the data to isolate the R-wave and the time point of local maximum for each suprathreshold peak was calculated. For each subject, this time point was determined at 1000 Hz (i.e to millisecond accuracy) and in this way all data were then encoded at the same sampling rate. For each block the time the touch-sensitive pads were contacted was extracted from the event channel and also resampled at 1000 Hz where necessary. For one subject there was a failure of the touch-sensitive pads and this subject was excluded from further analysis, leaving 25 subjects for data analysis.

Analysis of movements and phase of the cardiac cycle

To address whether or not there was a statistical relationship between the time the marble was placed on the touch-sensitive pad and the phase of cardiac cycle, we calculated the phase of the movement event as a function of the R-R interval[7]. Circular statistics were employed in order to exploit the repeating nature of the cardiac cycle. To this end, for each action endpoint the time of both the preceding and proceeding R-wave was calculated and the phase of the action endpoint was calculated as a function of the R-R interval in which it occurred (Figure 2A). For example, for an R-R interval of time $t_{R,}$ where the movement event occurred at time t_e the phase, in degrees, of that event was calculated as t_e/T_R x 360 (Figures 2B-C). For each subject, the mean phase was then calculated for the execution and observation blocks separately using circular averaging (Figure 2C). This resulted in two mean phases per subject, one for each condition (execution and observation). We then tested, separately for each condition, whether these phases differed from uniformity using Rayleigh tests. In addition, for qualitative comparison, we also calculated the distribution of phases in a circular histogram, where each bin was a 20th of a circle, normalized these so each bin represented the proportion of total events and averaged these distributions across subjects for execution and observation conditions. The first analysis shows the uniformity of the mean phase across subjects but gives no indication of the degree of uniformity of the phases for each subject, which is shown by the second analysis.

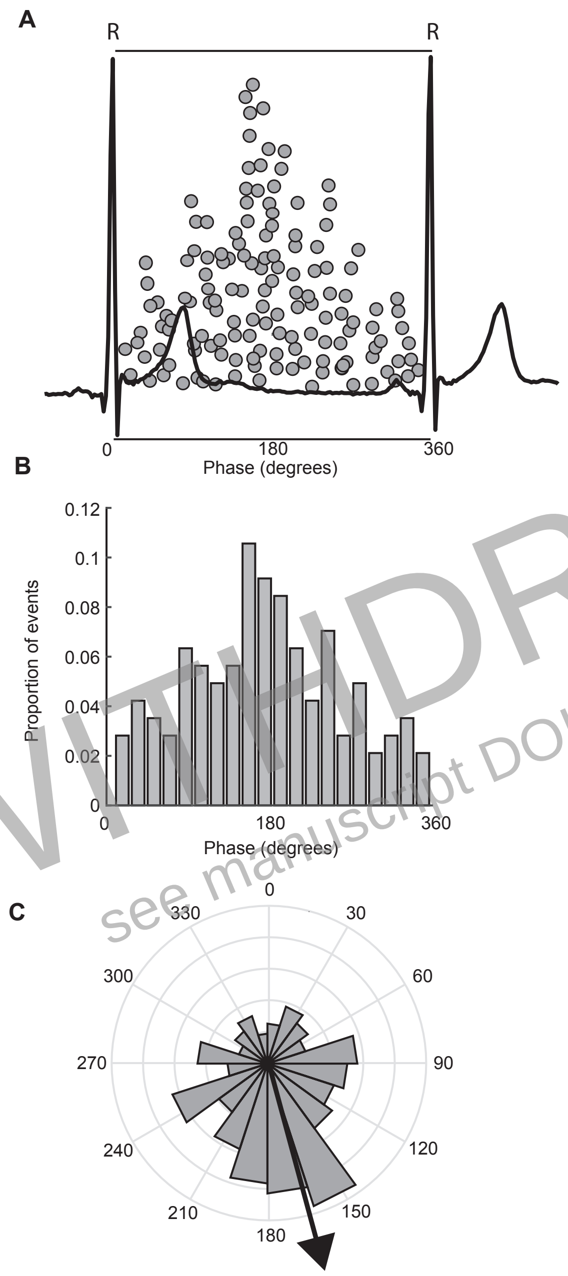

Figure 2: *Individual subject data analysis. This figure shows the data from a single representative subject during the action execution task. Panel A) shows the time of occurrence of every motor event as a function of the R-R interval during the action execution condition. The events are shown at the phase of the R-R interval, in degrees. The events are superimposed on a representative R-R interval from the same subject. Panel B shows the histogram, in 20 bins, of the frequency of motor events in each phase bin. The y-axis shows the proportion of total events in each phase bin. Panel C) shows the same data as in (B) but in a circular histogram. The black arrow shows the mean phase of this circular data for this subject and condition.*

Results

Prior to testing our main hypothesis that there would be a relationship between movement timing and the phase of the cardiac cycle, we tested for a significant difference in the length of the cardiac cycle (operationalized as the R-R interval) between observation and execution conditions. We also tested whether there was a relationship between movement time in the execution and observation conditions and if there was a relationship between the length of the cardiac cycle and movement time.

There was no significant difference in the duration of the mean R-R interval between action execution and action observation (856.3 and 848.5 ms respectively; t(24) = 0.7376, p = 0.47). There was no significant linear correlation between mean R-R interval and mean movement time. This was non-significant for both action execution (r= -0.19, p = 0.37) (Figure 3A) and action observation (r= -0.25, p = 0.22) (Figure 3B). However, there was a significant linear correlation between movement time during action execution and movement time during action observation (r = 0.73 p < 0.005) (Figure 3C). This significant relationship is consistent with the hypothesis that a common movement speed was adopted by the dyad but that this was not intrinsically tied to the length of the cardiac cycle.

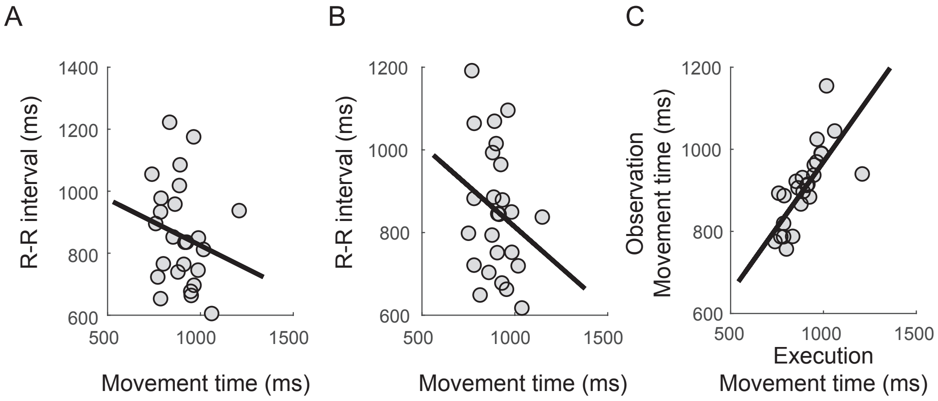

Figure 3: *Relationship between cardiac and movement parameters. Panels A&B show the relationship between the mean movement time and the mean R-R interval for each subject. In each*

panel the circles show the data from each subject and the solid line shows the line of best fit. Panel A shows the data during action execution and B shows the data during action observation. Panel C shows the relationship between the mean movement time for action observation and action execution. The significant positive relationship is consistent with the hypothesis that subjects imitated the movement speed of the other. In each panel each circle shows the data from one subject.

R-R interval results

The main aim of this study was to test whether there was evidence of a consistent phase relationship between the timing of movement events and the cardiac cycle both when performing actions and when observing someone else perform them. During action execution, the end of each movement occurred on average between heartbeats (mean 163.3^{o}, Figure 4A). This distribution differed significantly from the uniform distribution (Rayleigh test $z = 8.45$, $p < 0.0005$). Consistent with this, the mean distribution of the phase of all events across subjects during action execution mirrored the group level results (Figure 4C). The distribution was positively skewed around ~180^{o} and negatively skewed at the time of the R-peak, 0^{o}. In other words, the distributions were skewed from a uniform circular distribution.

The corresponding analysis for observed actions showed a similar pattern. On average, the observed movement also ended between heartbeats, with a phase of 185.5^{o} (Figure 4B). This distribution differed significantly from the uniform distribution (Rayleigh test $z = 4.68$, $p = 0.0081$). As with the phase relationship for action execution, the mean distribution of the phase of all events across subjects during action execution mirrored the group level results (Figure 4D). The distribution was positively skewed around ~180^{o} and negatively skewed at the time of the R-peak and extending into the first quarter of the R-R interval.

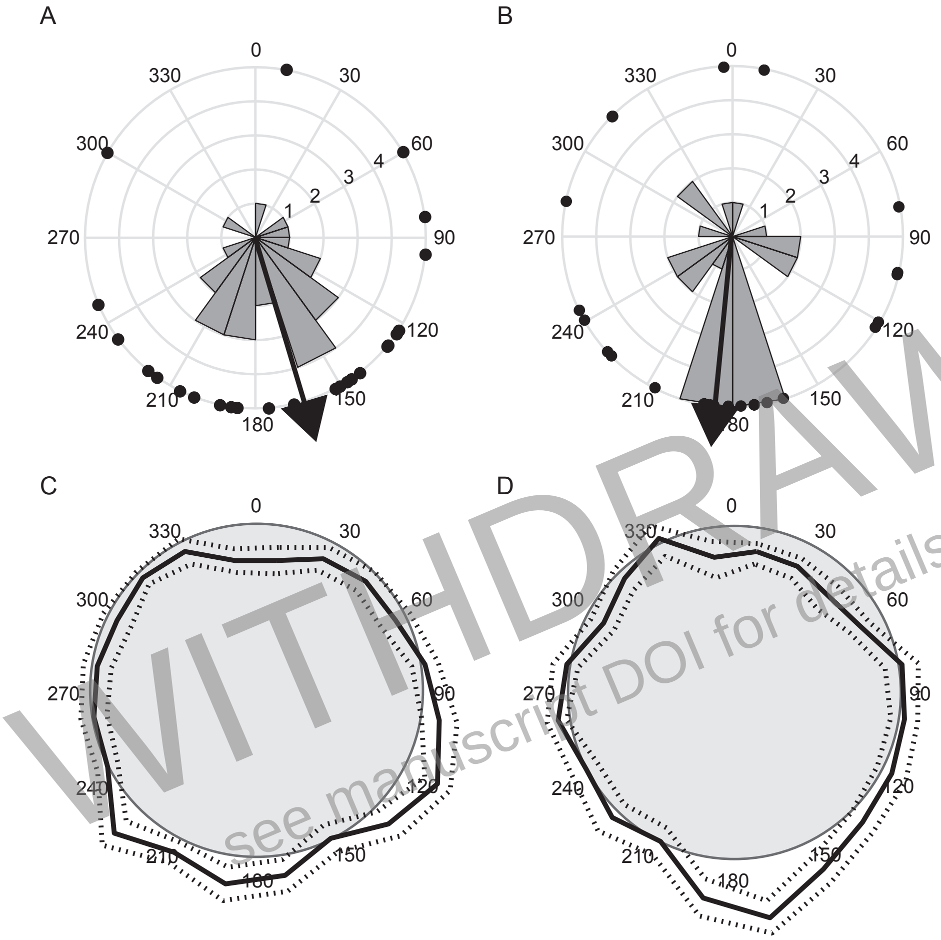

Figure 4: *Relationship between time of movement culmination and cardiac cycle. Panels A-D show the relationship between the time of the movement event (action end point) with respect to the phase of the R-R interval. In each panel the R peaks occurred at 0*^{o} *and the phase through the R-R interval cycles clockwise round the circle. Panels A&C show the data for executed actions and Panels B&D show the data for observed actions. In Panel A&B the dots show the mean phase for each subjects. The circular histogram show the frequency of the data as a function of phase. The solid black arrow shows the circular mean phase across subjects. Panels C&D depict the distribution of the mean normalized circular histograms across subjects, demonstrating the conformity of the distribution across the sample. The circle shows a uniform distribution. The solid black line depicts the mean phase distribution and the dotted lines show the standard error around this mean. When the lines are outside the circle this indicates a positive skew (more likely than chance) and when inside a negative skew (less likely than chance).*

Discussion

Here, we showed that the timing of self-paced movements and phases of the cardiac cycle are linked in a similar way for both execution and observation. Movement end points were significantly less likely to occur during a heartbeat, synchronous with the R-peak, and significantly more likely to occur between heartbeats. This same relationship was also observed between the motor events of an actor and the cardiac cycle of an observer. That is, the observer was significantly less likely to experience a heartbeat when observing movement endpoints. Additionally, there was a significant positive correlation between movement time in execution and observation conditions, suggesting dyads adopted a common movement speed. These results build on previous separate literatures that find both a relationship between discrete motor events and cardiac timing, and cardiac synchronicity between interacting individuals.

Many have suggested that an internal central pacemaker guides the timing of motor actions[1,2,33,34]. The heart, with its regular rhythmicity that modulates with arousal level, intuitively represents a good candidate for this role. Indeed, there is evidence that stimulation of afferent vagal and glossopharyngeal pathways is associated with modulations of efferent motor pathways. For example, pressure applied to the carotid sinus, which modulates baroreceptor firing[35], inhibits spontaneous movements and reduces muscle tone in anaesthetized animals[36]. The benefits of timing behaviour to the cardiac cycle, however, remain unknown. It is possible that as agents, we act upon the environment such that relevant signals appear during optimal phases of the cardiac cycle[7]. It may be that stimuli whose processing would benefit from information on the state of cardiovascular arousal are more acutely perceived at systole, when baroreceptor feedback occurs, while stimuli that would not benefit from such signalling are better processed during diastole. As such, during systole, fearful faces are more readily detected, and result in greater amygdala activation[5], and race-related threat appraisal is heightened[37]. Meanwhile, during diastole, target shooting[38,39] and memory for words[40] is more accurate. The current results suggest we may act upon our environment in such a way as to maximize this interoceptive distinction.

In the present study, we not only observed a relationship between the cardiac cycle and action execution, but also observed a similar relationship for action observation. It has been suggested that action observation results in the observer’s motor system generating a model of how they would perform it[27], facilitating action understanding. It is possible that inference about the mental states of others is concurrently supported by a form of interoceptive mirroring. Such a mechanism might explain how, in the present data, action observation resulted in a similar movement-cardiac rhythm to that seen in the individual executing the action. As the observer’s motor system predicts the actor’s next movements, comparable physiological conditions are simulated, much like action observation results in an increase in excitability in the muscles required to perform the observed action[26].

The mutual prediction of each other’s’ actions is thought to facilitate joint coordinated action and the achievement of shared goals[41,42,43]. There is evidence to suggest that shared representations of action form automatically even when no joint action is required and it would be more effective to ignore the other person[44]. The results found here suggest the possibility that cardiac-movement synchronicity may support the interpersonal coordination that underlies joint action, through physiological attunement. Such coordination may serve as “social glue”, fostering feelings of group belonging and closeness[45]. A number of findings appear to support this. Professional interviewers’ judgements of trainees’ competence have been found to correlate positively with the trainees’ convergence of speech rate and response latency[46]. The degree of convergence appears to vary based on personality traits and social standing. For example, participants who scored higher on a measure of the need for social approval converged more to their partner’s speech intensity and pause length than participants who scored lower[47]. Moreover, greater language convergence is observed towards occupational superiors than subordinates, in that foremen converge more to the language of managers. Increased physiological covariation, in the form of galvanic skin response (GSR) has been observed in dyads who either like or dislike each other, compared to those who hold neutral opinions of each other[48]. Future work should seek to investigate whether inter-dyad factors such as inter-individual liking and physical similarity to one's partner, or individual differences such as personality traits, are predictive of the cardiac-movement synchronicity effect observed here.

It has been argued that a dysfunction in movement dynamics would have implications for the experience of social connectedness[49]. Individuals who do not attend to the dynamics of others' movements, either due to a lack of ability or motivation, are likely to feel less social connectedness when engaging in joint activities. Engaging in synchronous joint action may foster cognitive benefits. Synchronicity may engage the same neural processes that allow access to others' mental states[50,51,52]. This is in line with data suggesting that high-empathy individuals sow greater non-conscious mimicry of others, termed the 'chameleon effect'[53]. Perhaps tellingly, the severity of positive symptoms (hallucinations and delusions) in schizophrenia is inversely correlated to the degree of movement synchronicity the individual displays in conversation with a partner[54]. Autistic children show significantly less in-sync rocking with a caregiver than neurotypical children in a rocking chair paradigm[55] and engage in briefer turn-taking sequences than other children[56].

Important questions remain regarding precisely under what conditions heart and movement synchronicity occurs. Understanding this may aid in interpreting previous findings that report no relationship between the heart and movement[57]. At the level of a single subject, it is likely that not all centrally mediated sensorimotor events show a phased relationship with the heart. In dyads, possible mediators include the history of interpersonal interaction, speech coordination, the structure of the task and the dynamics of turn taking, and the degree of behavioural coordination between the agents[18]. It is perhaps noteworthy that in the present study, many of the subjects reported during debriefing that they found replicating the sequence of movements challenging. The cognitive demands of the task may be an essential difference between the present design and other studies that report no relationship between heart and movement.

In summary, these findings demonstrate a phasic relationship between the timing of motor events and the cardiac cycle in both action execution and observation. These results suggest that interoceptive signals from the heart and self-paced movement are intrinsically linked. The observation of this phasic relationship both when executing and observing action raises the possibility that this phasic relationship may be driving interpersonal synchronicity, which has been found to foster successful social interaction.

References

1. Coleman, W. M. The psychological significance of bodily rhythms. *J. Comp. Psychol.*, **1,** 213. (1921).
2. Anders, P. Über den individuellen Eigenrhythmus beim menschlichen Gange und seine Beziehungen zum Rhythmus der Herz- und Atemtätigkeit. *Pflügers Archiv*, **220,** 287 -299. (1928).
3. Levy, M. N., Martin, P. J., Iano, T., & Zieske, H. Effects of single vagal stimuli on heart rate and atrioventricular conduction. *Am. J. Physiol.*, **218,** 1256-1262 (1970).
4. Reid, J. V. O. The cardiac pacemaker: Effects of regularly spaced nervous input. *Am. Heart J.*, **78,** 58-64 (1969).
5. Garfinkel, S. N. et al. Fear from the heart: Sensitivity to fear stimuli depends on individual heartbeats. *J. Neurosci.*, **34,** 6573-6582 (2014).
6. Fiacconi, C. M., Peter, E. L., Owais, S., & Köhler, S. Knowing by heart: Visceral feedback shapes recognition memory judgments. *J. Exp. Psychol.*, **145,** 559 (2016).
7. Kunzendorf, S. et al. Active information sampling varies across the cardiac cycle. *Psychophysiology*, e13322. (2019).
8. Lacey, J. I., Kagan, J., Lacey, B. C., & Moss, H. A. The visceral level: Situational determinants and behavioral correlates of autonomic response patterns. *Expression of the Emotions in Man*, **9**. (1963).
9. Lacey, J. I., & Lacey, B. C. Some autonomic-central nervous system interrelationships. *Physiological Correlates of Emotion*, 205-227. (1970).
10. Birren, J. E., Cardon, P. V., & Phillips, S. L. Reaction time as a function of the cardiac cycle in young adults. *Science*, **140** (1963).
11. Jennings, J. R., van der Molen, M. A., Brock, K., & Somsen, R. J. M. On the synchrony of stopping motor responses and delaying heartbeats. *J. Exp. Psychol. Hum. Percept. Perform.*, **18,** 422-436 (1992).
12. Rae, C. L. et al. Response inhibition on the stop signal task improves during cardiac contraction. *Sci. Rep.*, **8,** 9136. (2018).
13. Lacey, B. C., & Lacey, J. I. Two-way communication between the heart and the brain: Significance of time within the cardiac cycle. *Am. Psychol.*, **33,** 99. (1978).
14. Condon, W. S., & Ogston, W. D. Speech and body motion synchrony of the speaker-hearer. *The Perception of Language*, 150-184. (1971).
15. LaFrance, M. Posture mirroring and rapport. In M. Davis (Ed.), *Interaction Rhythms: Periodicity in Communicative Behavior,* (pp. 279-298). New York, NY: Human Scientific Press. (1982).
16. Shockley, K., Santana, M. V., & Fowler, C. A. Mutual interpersonal postural constraints are involved in cooperative conversation. *J. Exp. Psychol. Hum. Percept. Perform.*, **29,** 326. (2003).

17. Dale, R., Fusaroli, R., Duran, N. D., & Richardson, D. C. Chapter 2 - The self-organization of human interaction. *Psychol. Learn. Motiv.*, **59,** 43-95. (2013).

18. Fusaroli, R., Bjørndahl, J. S., Roepstorff, A., & Tylén, K. A. Heart for Interaction: Shared Physiological Dynamics and Behavioral Coordination in a Collective, Creative Construction Task. *J. Exp. Psychol. Hum. Percept. Perform.*, **42,** 1297. (2016).

19. Konvalinka, I et al. Synchronized arousal between performers and related spectators in a fire-walking ritual. *Proc. Natl. Sci. U. S. A.*, **108,** 8514-8519. (2011).

20. Levenson, R. W., & Gottman, J. M. Marital interaction: physiological linkage and affective exchange. *J. Pers. Soc. Psychol.*, **45,** 587. (1983).

21. Levenson, R. W., & Ruef, A. M. Empathy: A physiological substrate. *J. Pers. Soc. Psychol.*, **63,** 234. (1992).

22. Elkins, A. N., Muth, E. R., Hoover, A. W., Walker, A. D., Carpenter, T. L., & Switzer, F. S. Physiological compliance and team performance. *Appl. Ergon.*, **40,** 997-1003. (2009).

23. Henning, R. A., Boucsein, W., & Gil, M. O. Social-physiological compliance as a determinant of team performance. *Int. J. Psychophysiol.*, **40,** 221-232. (2001).

24. Henning, R. A., & Korbelak, K. T. Social-psychophysiological compliance as a predictor of future team performance. *Psychologia*, **48,** 84-92. (2005).

25. Strang, A. J., Funke, G. J., Russell, S. M., Dukes, A. W., & Middendorf, M. S. Physio-behavioral coupling in a cooperative team task: Contributions and relations. *J. Exp. Psychol: Hum. Percept. Perform.*, **40,** 145-158. (2014).

26. Gallese, V., & Goldman, A. Mirror neurons and the simulation theory of mind-reading. *Trends Cogn. Sci.*, **2,** 493-501. (1998).

27. Press, C., Heyes, C., & Kilner, J. M. Learning to understand others' actions. *Biol. Lett.*, **7,** 457-460. (2011).

28. Wicker, B. et al. Both of us disgusted in my insula: the common neural basis of seeing and feeling disgust. *Neuron*, **40**, 655-664. (2003).

29. Ondobaka, S., Kilner, J., & Friston, K. The role of interoceptive inference in theory of mind. *Brain Cogn.,* **112,** 64-68. (2015).

30. Lacey, B. C., & Lacey, J. I. Change in heart period: A function of sensorimotor event timing within the cardiac cycle. *Physiol. Psychol.*, **5** (1977).

31. Xygalatas, D., Konvalinka, I., Bulbulia, J., & Roepstorff, A. Quantifying collective effervescence: Heart-rate dynamics at a fire-walking ritual. *Commun. Integr. Biol.*, **4,** 735-738 (2011).

32. Hale, J., Ward, J. A., Buccheri, F., Oliver, D., & Hamilton, A. Are you on my wavelength? Interpersonal coordination in naturalistic conversations. Preprint at: https://psyarxiv.com/5r4mj/download?format=pdf (2018).

33. McCraty, R., Atkinson, M., Tomasino, D., & Bradley, R. T. The coherent heart: Heart-brain interactions, psychophysiological coherence, and the emergence of system-wide order.

Integral Review: A Transdisciplinary & Transcultural Journal for New Thought, Research, & Praxis, **5**. (2009).

34. Treisman, M., Faulkner, A., Naish, P. L., & Brogan, D. The internal clock: Evidence for a temporal oscillator underlying time perception with some estimates of its characteristic frequency. *Percept.*, **19,** 705-742. (1990).
35. Mancia, G., & Mark, A. L. Arterial baroreflexes in humans. In J. T. Shepherd & F. M. Abboud (Eds.), *Handbook of Physiology, Section 2: The Cardiovascular System* (pp. 755-793). Bethesda, MD: American Physiological Society. (1983).
36. Koch, E. Die reflektorische selbststeuerung des kreislaufes. In *Ergebnisse der Kreislaufforschung*. E. Kisch (Ed.). Dresden: Steinkopff. (1931).
37. Azevedo, R. T., Garfinkel, S. N., Critchley, H. D., & Tsakiris, M. Cardiac afferent activity modulates the expression of racial stereotypes. *Nat. Commun.*, **8,** 13854. (2017).
38. Bellamy, M., Collins, D., Holmes, P., & Loze, G. Shot patterns in ECG recordings for elite air-pistol shooters. *Journal of Sports Sciences, Conference Communications*, **17,** 48-49. (1999).
39. Bothwell, S., Donne, B., & Andrews, J. F. Does heart rate or phase of cardiac cycle at triggering affect the performance of elite marksmen? Journal of Physiology – London, **501,** 6. (1997).
40. Garfinkel, S. N. et al. What the heart forgets: Cardiac timing influences memory for words and is modulated by metacognition and interoceptive sensitivity. *Psychophysiology*, **50,** 505-512. (2013).
41. Flanagan, J. R., & Johansson, R. S. Action plans used in action observation. *Nat.*, **424,** 769. (2003).
42. Kilner, J. M., Vargas, C., Duval, S., Blakemore, S. J., & Sirigu, A. Motor activation prior to observation of a predicted movement. *Nat. Neurosci.*, **7,** 1299. (2004).
43. Verfaillie, K., & Daems, A. Representing and anticipating human actions in vision. *Vis. Cogn.*, **9,** 217-232. (2002).
44. Sebanz, N., Knoblich, G., & Prinz, W. Representing others' actions: just like one's own? *Cogn.*, **88,** B11-B21. (2003).
45. Lakin, J. L., Jefferis, V. E., Cheng, C. M., & Chartrand, T. L. The Chameleon Effect as Social Glue: Evidence for the Evolutionary Significance of Nonconscious Mimicry. *J. Nonverbal Behav.*, **27,** 145–162. (2003).
46. Street Jr, R. L. Speech convergence and speech evaluation in fact-finding interviews. *Hum. Commun. Res.*, **11,** 139-169. (1984).
47. Natale, M. Convergence of mean vocal intensity in dyadic communication as a function of social desirability. *J. Pers. Soc. Psychol.,* **32,** 790. (1975).
48. Kaplan, H. B., Burch, N. R., & Bloom, S. W. Physiological covariation and sociometric relationships in small peer groups. In P. H. Leiderman & D Shapiro (Eds.), *Psychobiological Approaches to Social Behavior*. Stanford, CA: Stanford University Press. (1964).

49. Marsh, K. L., Richardson, M. J., & Schmidt, R. C. Social connection through joint action and interpersonal coordination. *Top. Cogn. Sci.*, **1,** 320-339. (2009).

50. Hutchins, E. *Cognition in the Wild.* London: MIT press. (1995).

51. Semin, G. R. Grounding communication: Synchrony. In A. W. Kruglanski & E. T. Higgins (Eds.), *Social Psychology: Handbook of Basic Principles* (pp. 630-649). New York, NY: Guilford Press. (2007).

52. Semin, G. R., & Cacioppo, J. T. Grounding social cognition: Synchronization, entrainment, and coordination. In G. R. Semin & E. R. Smith (Eds.), *Embodied Grounding: Social, Cognitive, Affective, and Neuroscientific approaches* (pp. 119-147). New York, NY: Cambridge University Press. (2008).

53. Chartrand, T. L., & Bargh, J. A. The chameleon effect: the perception–behavior link and social interaction. *J. Pers. Soc. Psychol.*, **76,** 893. (1999).

54. Kupper, Z., Ramseyer, F., Hoffmann, H., & Tschacher, W. Nonverbal synchrony in social interactions of patients with schizophrenia indicates socio-communicative deficits. *PLoS one*, **10,** e0145882. (2015).

55. Marsh, K. L., Richardson, M. J., & Schmidt, R. C. Social connection through joint action and interpersonal coordination. *Top. Cogn. Sci.*, **1,** 320-339. (2009).

56. Mundy, P., Sigman, M., Ungerer, J., & Sherman, T. Defining the social deficits of autism: The contribution of non-verbal communication measures. *J. Child Psychol. Psychiatry,* **27,** 657-669. (1986).

57. Wallot, S., Mitkidis, P., McGraw, J. J., & Roepstorff, A. Beyond synchrony: joint action in a complex production task reveals beneficial effects of decreased interpersonal synchrony. *PloS one*, **11,** e0168306. (2016).