"The hidden rhythm of interpersonal (sub-)movement coordination"
No.246/20

Final Scientific Report

Background and aims

Movement is organized into smaller units, or primitives (Hogan and Sternad, 2012) – submovements – which combine together to make up full kinematic trajectories (Navas and Stark, 1968, Miall et al., 1993). If observed under the appropriate lens, continuous (non-ballistic) movement is never really smooth, and its elementary units become appreciable as discontinuities in the kinematic profile. Despite being most often filtered out in movement analysis, such discontinuities, or speed breaks are not a consequence of biomechanical constraints, nor an incidental or erratic phenomenon but tend to recur with specific periodicity in the range of 2-3 Hz. The presence of submovements has first been noticed more than a century ago (Woodworth, 1899); since then, submovements have been documented in many studies, in human (Miall et al., 1993, Doeringer and Hogan, 1998, Pasalar et al., 2005) as well as non-human primates (Miall et al., 1986, Roitman et al., 2004, Hall et al., 2014, Susilaradeya et al., 2019), and generally ascribed to an intermittent control of movement, deemed as an efficient computational strategy to allow optimal use of sensory feedback in the face of inherently long sensorimotor delays (Navas and Stark, 1968, Craik, 1947, Neilson et al., 1988, Sakaguchi et al., 2015, Gawthrop et al., 2011). Submovements are thought to consist in pre-programmed (open loop) motor corrections that are being generated in an intermittent fashion. Their dependence on sensory feedback is however unclear (Doeringer and Hogan, 1998, Miall et al., 1993, Vallbo and Wessberg, 1993). Artificially increasing feedback delays during visuomotor control tasks (such as hand tracking of a visual target) alter submovement frequency in a consistent manner (Miall, 1996, Susilaradeya et al., 2019, Miall et al., 1985). Yet, submovements seem not to be just a mere consequence of extrinsic delays in the visuomotor loop. Recent evidence highlights how the intrinsic oscillatory dynamics within the motor system contributes as well (Hall et al., 2014, Pereira et al., 2017, Jerbi et al., 2007), and in a way that is partly independent from (experimentally manipulated) feedback delays (Susilaradeya et al., 2019). Submovements may thus arise from a more complex interplay between intrinsic and extrinsic constraints on visuomotor loop dynamics (Susilaradeya et al., 2019).Interpersonal coordination requires continuous corrections based on an accurate (and mostly visually mediated) estimation of others' behaviour towards a joint motor outcome. For such coordination to be successful, information must be flowing within both individual and inter-individual action-perception loops. This project leverages on movement intermittency to open an empirical window upon these action-perception loops, providing the opportunity for a mechanistic understanding of interpersonal neuro-behavioural coordination.

Methods

Participants

A total of 40 participants (26 females; age: 24±3.6 years, MEAN±SD) were recruited for the study. Participants took part in Session 1 (Solo task) and were randomly paired to form couples matched by gender and participate in Session 2 (Dyadic task) of the experiment. All participants were right-handed (by self-report) and had normal or corrected-to-normal vision. Following an explanation of the study and experimental procedures, participants provided written informed consent in accordance with the guidelines of the local ethics committee (Comitato Etico di Area Vasta Emilia Centro, approval number: EM255-2020_UniFe/170592_EM Estensione) and the Declaration of Helsinki. At the end of the experiment, participants were reimbursed with for their participation (€12 per hour).

Experimental procedure

Session 1 – Solo task

Participants were comfortably seated and held their right forearm with the ulnar side resting on a table in front of them. They were asked to perform rhythmic flexion-extension movements around the metacarpophalangeal joint with their right index finger while seeing (vision) or not seeing (no vision) their own hand. In the 'no vision' condition, the hand was hidden from view by a black panel. We instructed participants to keep a slow regular movement pace of ~15 bpm (flexion/extension movement duration: 2 s; whole flexion-extension cycle: 4 s). To internalize the reference pace, they underwent a brief familiarization phase (~2min) before the experiment in which they practiced with a metronome; the

metronome was then played for only a few seconds to refresh the participants' memory before each experimental condition. During the actual recording sessions, the metronome was silenced and, therefore, participants' movements were self-paced.

Session 2 – Dyadic task

Two participants were seated at a table facing each other (~1 m apart) on opposite sides of a panel, which prevented them from seeing each other's faces (Figure 1). They were asked to maintain a posture similar to that described for the solo task, but with their right index finger pointing straight toward their partner's corresponding finger. Participants were asked to perform rhythmic flexion-extension movements with the right index fingers, moving as synchronously as possible with their partner toward the same direction (in-phase) or opposite directions (anti-phase; see Figure 1). The experimental procedure was identical in all other aspects (e.g., instructed pace of movement, familiarization with the metronome) to that described for the solo task.

EEG data recording

Dual-EEG data were recorded continuously during the experiment with two 64-channel active electrode systems (Brain Products GmbH, Gilching, Germany). Electrooculograms (EOGs) were recorded using 4 electrodes from the cap: FT9, FT10, PO9, and PO10 were removed from their original scalp sites and placed at the bilateral outer canthi and below and above the right eye to record horizontal and vertical eye movements, respectively. All electrodes were online referenced to the left mastoid. The impedance of the electrodes was kept below 15 kΩ. EEG signals were sampled at 1000 Hz.

Kinematic data recording

The 3D finger position was measured using a motion capture system with ten cameras (Vicon Nexus, RRID:SCR_015001; sampling rate: 300 Hz). Retro-reflective markers were placed on the distal phalanx of the right index finger (marker diameter: 6.4 mm). Additional markers (diameter: 9.5 mm) were placed on the metacarpophalangeal joint and the styloid process of the radius to ensure that participants kept their wrist still during the task. Recording of kinematic data was managed through the Vicon recording software (Nexus) and initiated at the beginning of each trial (see Data collection) via a TTL signal (recording was interrupted at the end of the trial, i.e., after 2'1''). The same TTL was also sent to the EEG recording system to accurately synchronize the EEG and kinematic data.

Data collection

Data were collected in separate trials during which participants performed the task (Solo – vision, Solo – no vision, Dyadic – in-phase, Dyadic – anti-phase) continuously for 2 min. Participants repeated 3 trials (of 2 min each) for each task and experimental condition (vision/no vision; in-phase/anti-phase), with short breaks in between. Condition order was randomized across participants/couples.

<u>Data analysis</u>

Analyses were performed with MATLAB using custom-made code and the FieldTrip toolbox. Kinematic analysis was restricted to the finger endpoint (i.e., marker placed on the fingertip) and its principal axis of movement – i.e., the x-axis (medio-lateral direction of motion). Continuous EEG data were first cut in 2-minute time series corresponding to individual trials, bandpass filtered (0.1-150 Hz; two-pass Butterworth filter, third order for each single pass), down sampled to 300 Hz (same sampling rate as kinematic data) and re-referenced (linked mastoids). EEG data were further cut into 4-second segments and manually checked for bad channels and/or artifacts in the time domain. Corrupted/noisy segments were discarded from further analysis either on an individual (Solo task) or pairwise basis (Dyadic task). Independent component analysis (ICA) was then used to identify and remove residual artifacts in the EEG signal related to eye movements and heartbeat. Bad channels were excluded from ICA and subsequently interpolated with a distance-weighted nearest-neighbor approach.

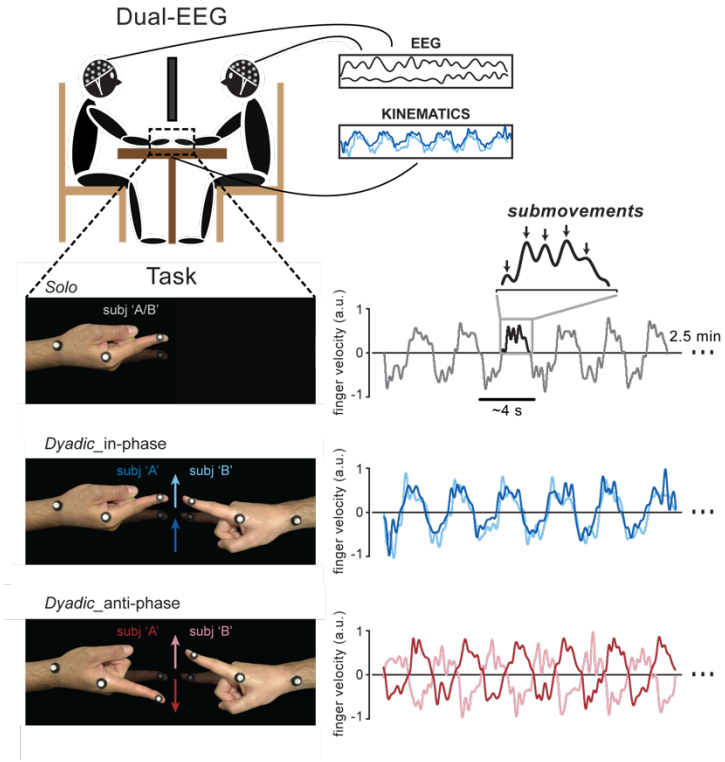

Figure 1. Task and experimental procedure. Dual-EEG (64-channel active electrode systems) and kinematic data (10-camera Vicon system) were recorded while participants performed rhythmic flexion-extension movements of the right index finger either alone (solo task) or together with a partner (dyadic task). The solo task was performed while seeing (vision) or not seeing one's own hand (not shown in the schematic); the dyadic task involved two different modes of coordination: towards the same direction as the partner (in-phase) or towards opposite directions (anti-phase).

Results

Kinematics

The microstructure of movement

The kinematics analysis confirms the results obtained in the behavioral study (Tomassini et al., 2022). Figure 2A shows the spectral analysis of the entire kinematic time series, indicating the presence of similar rhythmic components for all tested tasks/conditions. The largest peak at ~0.25 Hz corresponds to the instructed pace of movement. As expected on the basis of our previous study and in line with an extensive literature (e.g., Miall et al.,1993), a faster rhythmic component can also be observed at ~2-3 Hz, reflecting submovements. It is noteworthy that the component related to submovements is more clearly defined (producing a sharper peak) during dyadic in-phase coordination than anti-phase coordination or solo performance, most likely because of the greater relevance of applying recurrent visual-based motor corrections in this condition. Two additional but less interesting spectral components are present at ~0.7 Hz and ~8 Hz. The former seems to be harmonically related to the rhythmic movement pace, while the latter reflects physiological tremor (for a more extended discussion of these components see Tomassini et al., 2022).

Partners synchronize at the level of movement and submovement

Most importantly, when partners are required to coordinate their movements (dyadic task), their submovements are not generated in an independent fashion but in a systematic relationship to one another (Figure 2B). However, synchronization at the submovement level is highly dependent on the coordination mode and is only observed during in-phase coordination and not during anti-phase coordination, as evident from the frequency-resolved between-partners phase locking value (PLV) showing a clear (frequency-selective) increase at 2-3 Hz in the former but not the latter condition (Figure 2B). Notably, submovements are systematically alternated over time between the interacting partners, as if they reflected reciprocal online motor adjustments (Figure 3). As a sanity check, no consistent interpersonal synchronization is observed during solo performance (see Figure 2B, left panel).

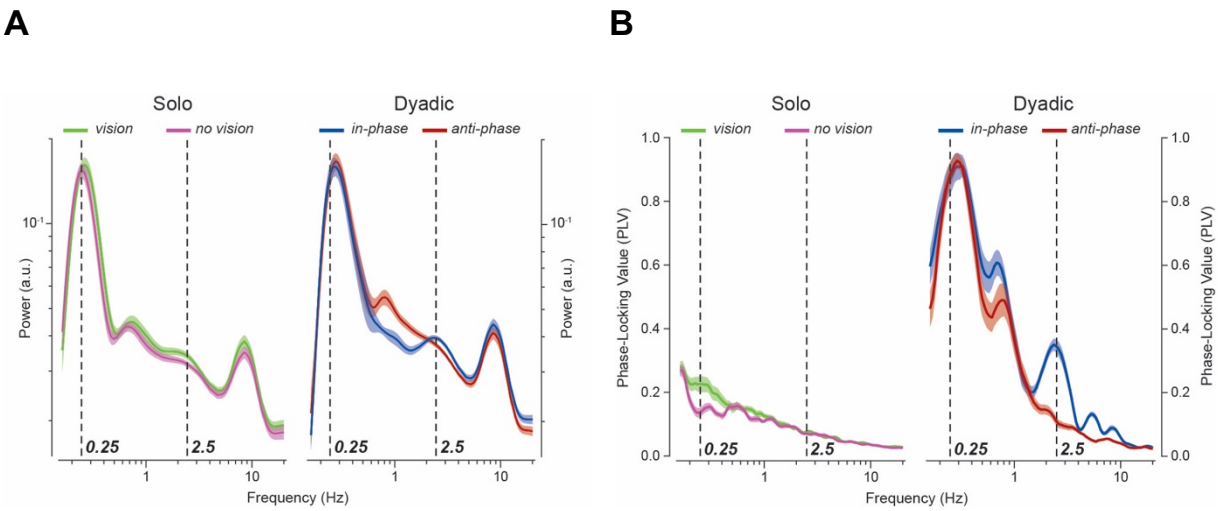

Figure 2. Kinematics results. A. Power spectrum of the kinematic time series shows distinct spectral peaks at the pace of movements (0.25 Hz) and at the frequency of submovements (2-3 Hz) in all tested tasks/conditions. Additional peaks are observed at ~0.7 and ~8 Hz, reflecting a harmonic of movement pace and physiological tremor, respectively (see also Tomassini et al., 2022). **B.** Phase-locking value (PLV) computed between the kinematics (velocity) of the two partners fingers for all tasks/conditions. A distinct increase in the PLV is observed at 2-3 Hz only for the dyadic in-phase coordination mode. No consistent PLV is expected during solo performance. The shaded areas represent ± SEM (standard error of the mean).

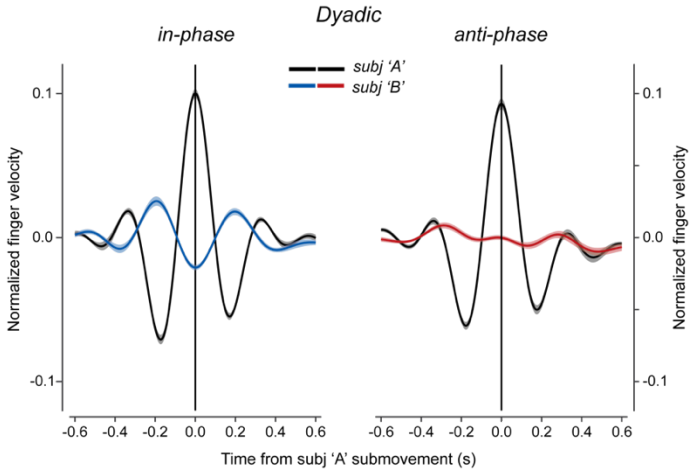

Figure 3. Submovement-locked analysis. Velocity for both partners – subjects ''A'' and ''B'' – time-locked to submovements generated by one partner in the couple – i.e., subject ''A'' by convention. Partners alternate submovements over time only during in-phase coordination (left panel) and not during anti-phase coordination (right panel).

Event-related potentials (ERPs)

Movement-related

As expected, the EEG activity is systematically modulated in relation to movement onset. Figure 4A,B shows the movement-related potential (or readiness potential) for the solo and dyadic task (data collapsed across experimental conditions). In line with the literature (Kornhuber HH and Deecke L, 1965), the EEG potential over frontocentral electrodes shows a negative component that begins long before movement onset (~1 s), slowly increases in amplitude reaching its peak at approximately -0.3 s, and then abruptly reverses its sign producing a large positive component that peaks shortly after movement onset (~0.15 s). Interestingly, the movement-related potential is modulated depending on whether movements are performed alone (solo task) or together with a partner (dyadic task), with a larger pre-movement negativity and post-movement positivity for the former and latter condition, respectively. We then examined whether the movement-related potential is modulated as a function of the experimental conditions (Figure 4C). The negative component is strongly modulated by the availability of the visual feedback. More specifically, when the visual feedback is not present (no vision)

the pre-movement modulation is much smaller than when the visual feedback is present (vision). Differently, no consistent modulation is observed as a function of the coordination mode (in-phase vs. anti-phase).

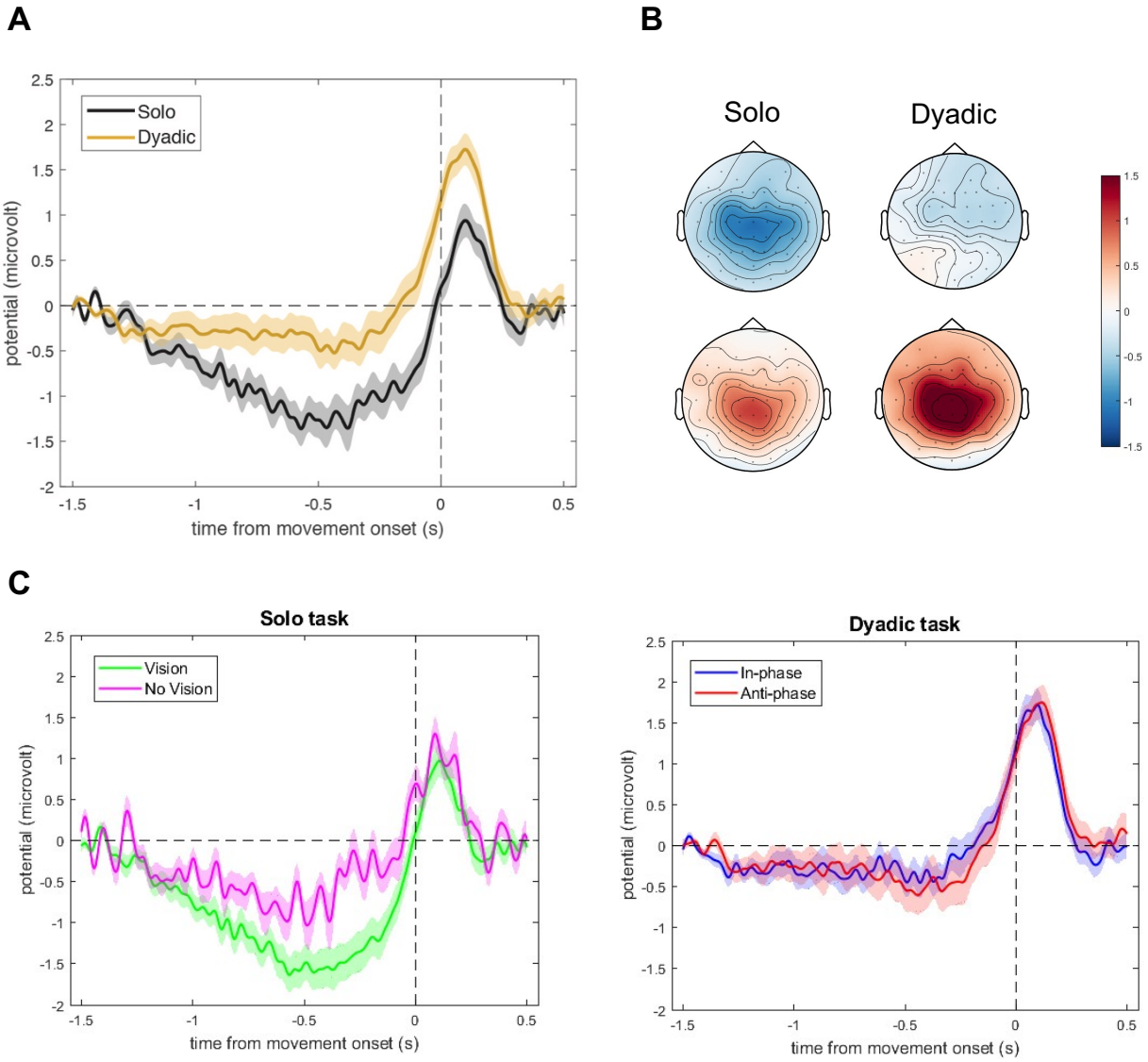

Figure 4. Movement-related EEG potential. **A.** Time course of the movement-related potential averaged across a subset of frontocentral electrodes (CPz, CP1, Cz, C1, FCz, FC1) for the solo (black) and dyadic (yellow) task (data collapsed across experimental conditions: vision/no vision, in-/anti-phase). **B.** Topographic maps for the negative (from -1.15 to -0.15 s; first row) and positive (from 0.05 to 0.15 s; second row) component of the movement-related potential for the solo (first column) and dyadic (second column) task. **C.** Time course of the movement-related potential averaged across a subset of frontocentral electrodes (CPz, CP1, Cz, C1, FCz, FC1) for the vision and no vision conditions in the solo task (left panel) and for the in-phase and anti-phase conditions in the dyadic task (right panel). The shaded areas represent ± SEM (standard error of the mean).

Submovement-related

Despite being very subtle changes in velocity, submovements are also associated with systematic modulations of EEG activity. Figure 5A shows the submovement-related potential for the solo and dyadic task (data collapsed across experimental conditions). Consistent with what reported in a recent study using a very different motor task (visuomotor tracking with a computer mouse, Pereira et al., 2017), the EEG potential shows a triphasic modulation: an increase before submovement generation (~-0.15 s), followed by a negative deflection (~0.1 s) and a later smaller increase (~0.3 s) after submovement generation. The first positive component shows slightly greater amplitude for the dyadic than for the solo task. Like the movement-related potential, the submovement-related modulation is

stronger for all components on the frontal and central electrodes, suggesting a somatomotor origin (Figure 5B). As with the movement-related potential, in the absence of visual feedback the potential shows smaller amplitude (especially for the positive components) than in the presence of visual feedback, while the coordination mode does not seem to affect the amplitude of the submovement-related potential (Figure 5C).

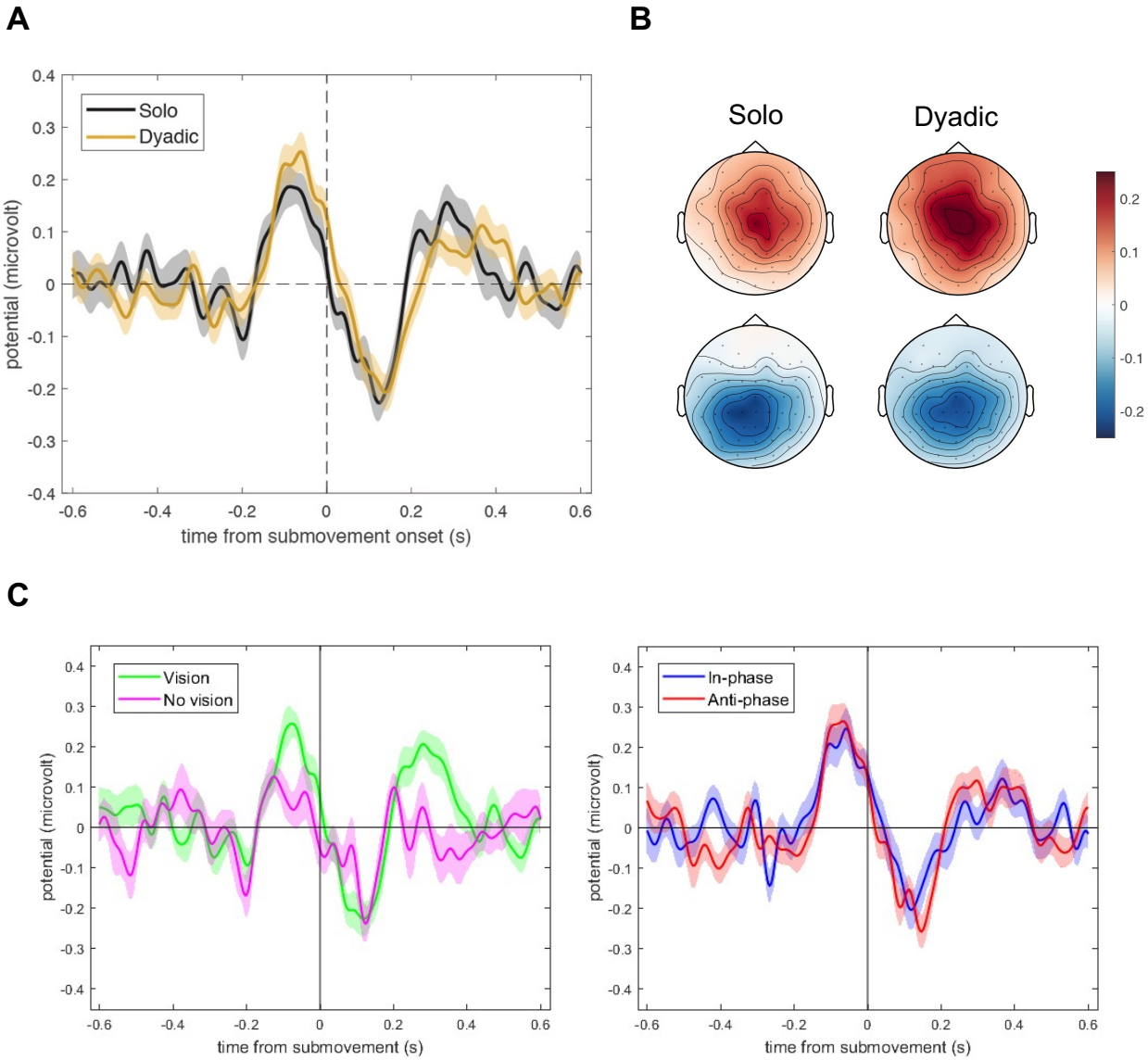

Figure 5. Submovement-related EEG potential. Time course of the submovement-related potential averaged across a subset of frontocentral electrodes (CPz, CP1, Cz, C1, FCz, FC1) for the solo (black) and dyadic (yellow) task (data collapsed across experimental conditions: vision/no vision, in-/anti-phase). **B.** Topographic maps for the early positive component (from -0.09 to -0.04 s; first row) and for the negative component (from 0.09 to 0.18 s; second row) of the submovement-related potential for the solo (first column) and dyadic (second column) task. **C.** Time course of the submovement-related potential averaged across a subset of frontocentral electrodes (CPz, CP1, Cz, C1, FCz, FC1) for the vision and no vision conditions in the solo task (left panel) and for the in-phase and anti-phase conditions in the dyadic task (right panel). The shaded areas represent ± SEM (standard error of the mean).

Most interestingly, EEG activities are systematically modulated not only in relation to one's own submovements but also to submovements generated by the partner. Figure 6 shows a sharp increase of the EEG potential occurring approximately 0.2 s after the partner's submovements. This modulation is maximal over parieto-occipital electrodes and can be observed for both coordination modes, although being slightly stronger for in-phase than anti-phase coordination. Importantly, several features of this EEG modulation, including latency, amplitude and topography, suggest that it is nontrivial, i.e., a simple

consequence of the systematic alternation of submovements between partners (Figure 3) combined with the presence of submovement-related potentials at the individual level (Figure 5).

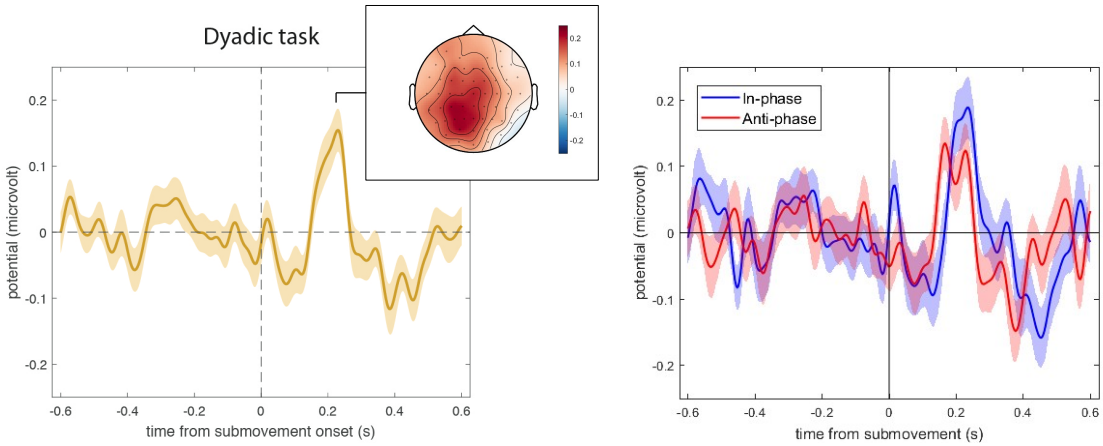

Figure 6. EEG potential evoked by the partner's submovements. EEG activity time-locked to submovements generated by the partner averaged across a subset of parieto-central electrodes (CPz, CP1, CP3, Pz, P1,P3) for the dyadic task (yellow), and separately for the in-phase (blue) and anti-phase (red) coordination modes. The topographic map is shown for data collapsed across coordination modes (from 0.19 to 0.23 s). The shaded areas represent ± SEM (standard error of the mean).

Cortico-kinematic coherence (CKC)

We also examined the frequency-resolved phase locking (PLV) between EEG activities and the kinematic data – otherwise called cortico-kinematic coherence (CKC) – as a function of their lag (i.e., relative time shift). Figure 7A shows that cortical activities are not only phase-locked to the rhythmic pace of the movements (~0.25 Hz), as reported in previous studies (Bourguignon et al., 2019), but also to the (quasi-)rhythmic generation of submovements (2-3 Hz). Intriguingly, the strength and topography of CKC is strongly modulated by the task (solo vs. dyadic) and experimental condition (vision vs. non vision, in-phase vs. anti-phase). More specifically, 2-3 Hz CKC is stronger when visual feedback is available and virtually null in the absence of visual feedback (despite submovements being present at the kinematic level, see Figure 2). CKC is also greater during in-phase than anti-phase coordination. The topographic distribution of coherence is mainly concentrated over the parietal electrodes contralateral to the effector (right hand), except that for the anti-phase condition, where coherence is more localized on the central midline electrodes (Figure 7B).

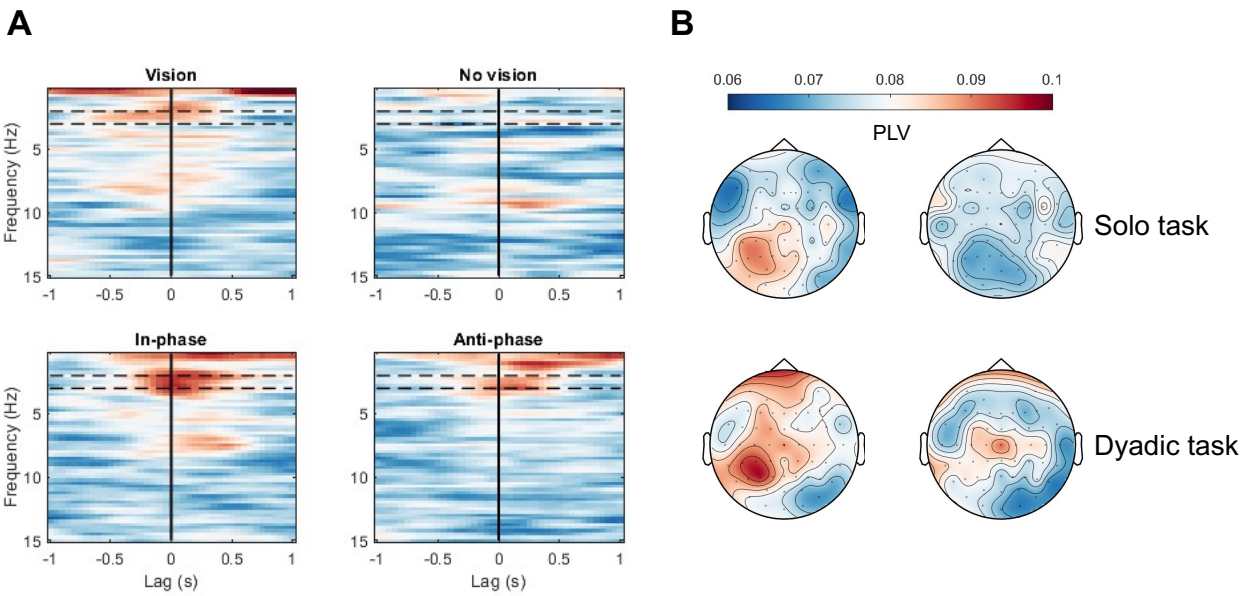

Figure 7. Cortico-kinematic coherence (CKC). A. Phase-locking value (PLV) computed between cortical activities and finger kinematics (same individual) for all tested tasks/conditions as a function of frequency and lag (relative timing between EEG and kinematic data). Negative/positive lags indicate that EEG activity precedes/follows in time finger kinematics. Dashed lines indicate the frequency range of submovements (2-3 Hz). **B.** CKC topographic maps for all tasks/conditions averaged for frequencies comprised between 2 and 3 Hz and lags comprised between -0.5 and +0.5 s.

Discussion

At the behavioral level, interpersonal movement coordination involves an implicit and automatic coupling of submovements between partners, which mainly occurs when motor coordination is effectively achieved through detection and correction of visuospatial errors. Here, we provide novel evidence for specific neural markers of submovements and their modulation as a function of the relevance and/or availability of visual feedback for both individual motor control and coordination with a partner. More specifically, we found that 1) submovement-related ERPs are greater when movements are performed in the presence than in the absence of visual feedback. Furthermore, although these are very subtle features, submovements generated by one's partner are reliably detected, as evidenced by the consistent modulation of parieto-occipital EEG activities time-locked to the partner's submovements, which further reinforces the idea that submovements are indeed used in vision-based motor coordination. We also found that 2) brain activities are consistently synchronized with one's own kinematics (CKC) on both the time scale of movements and submovements, but with a different topographic distribution. In fact, while CKC within the frequency range corresponding to the movement pace (0.25 Hz) is maximal on frontocentral electrodes (data not shown), CKC in the range of submovements (2-3 Hz) is mainly concentrated on parietal electrodes, suggesting that submovements are indeed regulated within a visuomotor loop. Consistent with this notion, CKC is virtually absent when visual feedback is not provided, and its parietal strength and distribution is highly modulated by the coordination mode, being greater when submovements play a key functional role in visuomotor control, i.e., during in-phase as opposed to anti-phase coordination.

Conclusions

In conclusion, this project contributed significantly to corroborating the evidence for consistent interpersonal coordination at the level of submovements (Tomassini et al., 2022). Most importantly, it provided new evidence on the neural machinery that controls the generation of submovements and its central role in achieving effective interpersonal coordination (Tomassini et al., in preparation). The present results represent an important first step toward a mechanistic understanding of how interpersonal motor coordination is achieved, based on the dynamical synchronization of processing that occurs within visuomotor loops. The principled choice of exploring the interpersonal neuro-behavioral dynamics through the lens of submovements has offered key insight on the mechanisms implicitly at play to align own coordinative structures to those of a partner, depending on task requirements. All in all, these mechanisms might represent an implicit low-level channel of sensorimotor communication on which basis motor coordination can be optimized.

Recommendations for future research

The activities and results stemming from the project raise a number of new questions, such as whether the macro- and microscopic architecture of movement is organized hierarchically, reflecting multiple nested sensorimotor loops, how this multiscale organization supports inter- but also intra-personal (of different body parts) coordination, and how it is shaped by multimodal sensory information (vision, proprioception, and audition). Many of these issues ultimately lead back to a central open question, namely, the cause-and-effect relationship that links micro- and macroscopic phenomena: whether coordination at the microscopic scale actually provides the building block of goal-directed behavioral organization at the macroscopic scale. To achieve this deeper mechanistic understanding, future investigation could make use of causal, interventional approaches to selectively perturb sensorimotor communication at microscopic levels and evaluate their causal contributions to macroscopic coordination performance. To this end, a virtualized version of the (inter-/intra-personal) motor coordination task could be implemented, which would allow to apply various online manipulations of the visual feedback provided to participants about their own and their partner's movement. In principle, a wide range of manipulations can be imagined. For example, one could make microscopic features (submovements) invisible or amplify them with the aim of disrupting or enhancing (inter-/intra-personal) communication within specific sensorimotor channels and on specific time scales.