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Across the Galaxy of Time

The role of Sensory Stimuli, Timing Mechanisms, and the Rhythmic Motor Performance

Playing on neuromuscular constraints underlying the control of the rhythmic movement

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Contributions of Author

Experiment I: Chapter 2

The design of the behavioural task was planned by Prof. Diego Minciacchi and by doctoral student (now Ph.D.) Claudia Del Tongo. Prof. Diego Minciacchi developed the goals of the study and planned the analyses collaboratively with Claudia Del Tongo. Prof. Alessandro Tognetti and Gabriele Dalle Mura planned and wrote the software for data collection, as well as the design and coding of MATLAB® software to analyze data. I recruited and tested participants. I performed the statistical analyses and wrote all sections of the manuscript with guidance and feedback from Prof. Minciacchi. The results of this experiments have been published on *Experimental Brain Research* Journal.

Experiment II: Chapter 3

I developed the goals of the study and planned the analyses collaboratively with Prof. Minciacchi. The design of the behavioural task, the data collection and scoring software were re-used from the Experiment I. I recruited and tested participants. I performed the statistical analyses. I wrote all sections of the manuscript with feedback from Prof. Minciacchi. The results of this experiments have been published on *Experimental Brain Research* Journal.

Experiment III: Chapter 4

I developed the goals of the study and planned the analyses. The design of the behavioural task, as well as the data collection and scoring software were re-used from the Experiment I and II. Prof. Anna Gottard performed the inferential statistical analyses. I recruited and tested participants. I wrote all sections of the manuscript collaboratively with Prof. Diego Minciacchi and Prof. Anna Gottard (contribution in Statistical Analysis and Results Sections). The results of this experiments have been published on *Frontiers in Systems Neuroscience* Journal.

Experiment IV: Chapter 5

I developed the goals of the study, the design of the behavioural task, and planned the analyses. The data collection software was re-used from the Experiment I, II, and III. Mr Alessio Martinelli refined the existing MATLAB® software to analyze data. I recruited and tested participants. I performed the statistical analyses. I wrote all sections of the manuscript with final supervision of Prof. Diego Minciacchi.

Experiment V: Chapter 6

I developed the goals of the study, the design of the behavioural task, and planned the analyses. The data collection software was re-used from the Experiment I, II, III, and IV. I recruited and tested participants. I performed the statistical analyses.

Experiment VI: Chapter 7

I developed the goals of the study, the design of the behavioural task, and planned the analyses. The data collection software was re-used from the Experiment I, II, III, IV, and V. I recruited and tested participants. I performed the statistical analyses. Neurological tests was performed by a neurologist, Prof. Diego Minciacchi.

Non enim numero haec iudicantur
These things are not judged by the number
Cicero, Rhetorica, De Officiis, II

Chapter 1: An Introduction to the Problem

1.1 General Overview

Time and space are the fundamental dimensions of our existence. In our today's social virtual world characterized by computer networks, cellular phone and virtual libraries space is gradually losing its value, while «time is becoming the essence of our times, as reflected by ever increasing speed, rate of return and productivity, concepts that are intrinsically related to time» (Buhusi and Meck, 2005). Humans process temporal information over a scale of at least 12 orders of magnitude (Mauk and Buonomano, 2004; Goel and Buonomano, 2014) with various orders degrees of precision. On the one extreme, we show to have daily physiological oscillations, such as our sleep-wake cycle, defined circadian rhythms that are controlled by molecular/biochemical oscillators. On the other extreme, we detect the delay required for sound to travel from one ear to the other, with such delays that are on the order of tens to hundreds of microseconds. However, temporal processing on the scale of tens and hundreds of ms is probably the most sophisticated and complex form of temporal processing, which is fundamental for motor control in walking, speech, playing or appreciating music, and participating in sports (Mauk and Buonomano, 2004; Buhusi and Meck, 2005).

The general aim of my research is the understanding of the mechanisms that underlie the control of the rhythmic voluntary movement, and how environmental stimuli, by effecting on the neuromuscular constraints, produce functional adaptations in the systems enrolled to control and stabilize sensorimotor coordination. In particular, my research is aimed to investigate whether and how timing mechanisms for the production of rhythmic movements are manipulable by environmental stimuli, and it explores whether a causal relationship subsists between the elicitation of a specific timing mode and the change of the precision performance.

In the world of excellence performance, the seeking of timing abilities can be explicit goal of practice schedules intended to achieve athletic or artistic perfection (van der Steen and Keller, 2013). It was shown that an increased precision of cadence consistency during running helps to improve running economy (Jan Bood et al., 2013). Moreover, it was demonstrated that after synchronized metronome training, a more coordinated movement dynamics during golf-swing performance was obtained (Sommer et al., 2014). In an artistic setting, by trying to identify movement properties that may support successful music performances, Goebl and Palmer found significant relationships between timing precision and efficient keystroke in piano performance (Goebl and Palmer, 2013; Watson, 2006).

Finally, in the pathological world, particularly in some motor disorders, timing abilities are reduced. For instance, it was revealed that patients with cerebellar lesions show increased timing variability when performing temporal production tasks, or during the production of isolated movements with a specified target duration (Spencer et al., 2003). Moreover, there is some task-specific movement disorders like musician's dystonia in which muscular incoordination, loss of voluntary motor control of refined movements, and alteration of timing parameters are exhibited (Altenmüller and Jabusch, 2009). Therefore, this research is expected to shift between basic and clinical research to translate the knowledge of mechanisms on healthy subjects into clinical neurorehabilitation proposes to manage/improve the movement in motor disorders where alterations of rhythmic motor performance, and abnormalities within and between the sensory and motor systems are typical pathological feature.

My research activity during the past four years, by using an experimental paradigm in which repetitive wrist's flexion-extensions are performed minimizing tactile and visual information, resulted in different tough largely interconnected studies.

Experiment I investigated whether and how non temporal and temporal characteristics of an auditory stimulus (presence, interval occupancy, and tempo) affect precision and accuracy of rhythmic motor performance.

In the Experiment II, with the inclusion of new recordings, the dataset of Experiment I was expanded to study whether simple and complex paced auditory stimuli (clicks and music, respectively) and their imaginations influenced in a different way the event-based and emergent timing, the timing mechanisms for the production of rhythmic actions. In addition, since the relationship linking the two forms of temporal control is a matter of debate we wanted to get a better insight on whether the two timing modes are mutually exclusive or whether an event-based component could coexist with an emergent component.

The Experiment III investigated whether the application of Kinesio taping, an elastic band used for treating athletic injuries, on the dominant motor effector was able to reduce the timing variability of repetitive rhythmic movements. We also attempted to understand whether a causal relationship subsisted between such reduction and functional augmentation of central structures involved, brought about by relieving, at least partially, structures from time control.

The Experiment IV evaluated whether Kinesio taping applied with different direction and tension on dominant motor effector might influence differently the precision of sensorimotor synchronization.

In the Experiment V was investigated the Impact of Kinesio taping in improving timing consistency of repetitive movements when it was applied on dominant and non-dominant hands. In addition, we studied whether different level of timing skills influences the neural processes governing the temporal regulation for production of rhythmic movements

In Experiment VI since the cerebellum is a strongly implicated structure in the processes of motor timing, an numerous studies have shown how cerebellar lesions determine an augmented variability in tasks of motor timing, was explored whether Kinesio taping, by modulating the timing processes employed for the production of movements, was able to improve the timing consistency of rhythmic movements on patients with spino-cerebellar ataxia.

1.2 Perception-action Interactions

The notion that perception is linked to action is not new. The famous sentence expressed by William James in his ideomotor theory of action: "every representation of a movement awakens in some degree the actual movement which is its object", dates back to the end of the nineteenth century (James, 1890).

More recently, McGurk and MacDonald (1976) demonstrated an influence of vision upon the auditory perception of spoken sounds (McGurk and MacDonald, 1976).

Further, Liberman and Mattingly (1985) hypothesized in their motor theory of speech perception that speech perception and speech production are intimately linked, assuming that hearing speech automatically activated the corresponding motor commands necessary to produce the sounds, ultimately facilitating the communication with interlocutor (Liberman and Mattingly, 1985).

A few years later, Decety speculated that mental representations during observation of actions performed by others, and even more during simulation of one's own actions, share common neural mechanisms with other covert aspects of motor performance, such as planning and programming, suggesting that there could be a motor aspect in the perceptual system (Decety, 1996).

Insights into the neural substrate of this motor simulation in perception came with the discovery of the mirror neuron system in the area F5 of premotor cortex in chimpanzees. These mirror neurons were described as a particular class of visuomotor neurons discharging both during the execution of a particular action and the observation of another individual (monkey or human) doing a similar action (Gallese et al., 1996; Rizzolatti et al., 1996), directly coupling perception to action.

These findings demonstrated that bodily states, perceptual systems and actions underlie information processing, supporting the viewpoint of "embodied cognition" that cognitive processes are deeply rooted in the body's interaction with the world, and challenging the classical cognitive theories that viewed the mind as an abstract information processor, and perceptual and motor systems not relevant to understanding "central" cognitive processes (Wilson, 2002).

Accordingly, it has been proposed a new framework for a more adequate theoretical treatment of perception and action planning, in which the planning or the execution of an action and the perception of its related sensory consequences are encoded in a shared representational medium (Prinz et al., 1997; Hommel et al., 2001). As a result, whenever one of the two components is activated, both motor and sensory areas in the brain are recruited. This combination of sensory and motor representations leads to the creation of internal models relative to the relationship between the two.

These models can either contain inverse or forward components (Wolpert et al., 1995). On the one hand, inverse models (also known as motor resonance) refer to the way perception activates the corresponding motor commands required for such sensory state to be achieved (e.g., Jeannerod, 1994; Prinz, 1997; Rizzolatti et al., 2001). On the other hand, forward models (also known as perceptive resonance) refer to the way actions activate sensory states. In other words, the system predicts the sensory outcomes of the executed or planned action (Davidson and Wolpert, 2005).

1.3 Auditory-motor Interactions

The same sensorimotor interactions were also observed in the audio-motor domain.

In the populations of mirror neurons it was found that some of them discharge when a specific action is performed and/or when the same action is heard or seen (Keysers et al., 2003), therefore representing actions independently of whether these actions are performed, heard or seen. This finding showed that the auditory modality can access the motor system.

Auditory–motor interaction may be defined as any engagement of auditory and motor systems, and may be conceptualized into two categories: feedforward and feedback.

In feedforward interactions, auditory system predominately influences the motor output, often in a predictive manner. An example is the phenomenon of tapping to the beat, where the listener during the synchronization phase anticipates with the movement the ongoing auditory stimulus (Repp and Su, 2013).

Feedback interactions are particularly relevant in musical performance in which the musician must listen to each note produced and implement appropriately timed motor adjustments to constantly control mutable pitch (Zatorre et al., 2007). Interestingly, it was shown that the manipulation of auditory feedback (Pfordresher and Palmer, 2006) altered motor performance: asynchronous feedback disrupts the timing of events, whereas alteration of pitch information disrupts the selection of appropriate actions, but not their timing (Zatorre et al., 2007). These studies indicate that disruptions occur since both actions and percepts depend on a single underlying mental representation (Zatorre et al., 2007), that is, a psychological construct describing information about an object, action or percept that is thought to be encoded in the brain.

Several fMRI studies were performed in pianists to specifically investigate the link between auditory and motor networks. In the study by Bangert and colleagueas, brain activity of trained pianists was evaluated during either listening to short piano melodies without no movements or pressing keys on a piano keyboard without auditory feedback. Study demonstrated that the neural regions engaged during the listen and play conditions overlapped, and included the supplementary motor and premotor areas, and planum temporale the superior temporal gyrus and the supramarginal gyrus, all areas involved in auditory-sensorimotor integration (Bangert et al., 2006).

A similar effect has been previously observed by Haueisen and Knosche (2001) that using magnetoencephalography (MEG) showed that pianists during passive listening to well-known melodies activated involuntary the contralateral primary motor (Haueisen and Knosche, 2001). Conversely, observation of silent piano playing additionally recruited auditory areas in pianists (Haslinger et al., 2005).

Finally, a transcranial magnetic stimulation (TMS) study also showed increased motor excitability in the primary motor cortex of pianists when they listened to a piano piece that they had rehearsed, compared with a flute piece on which they were untrained (D'Ausilio et al., 2006). These findings support the notion that the auditory and motor systems are tightly coupled.

1.4 Sensorimotor Synchronization

1.4.1 Evolution Hypothesis

Sensorimotor synchronization (SMS) is the rhythmic coordination of perception and action occurring in many contexts, from finger tapping in time with a metronome to dance and musical ensemble performance (Repp and Su, 2013). Generally, the term SMS refers to a situation in which the action is coordinated with a periodic predictable external stimulus, so that the predictability of the reference point results from its systematic repetition over the time.

Generally, basic mechanisms of SMS are studied by the use of the simple finger-tapping task in which subjects are asked to tap along to an identifiable repeating click or tone (Repp, 2005).

There are many alternatives to perform this task, arising from different form of movements (e.g., tapping with or without tactile opposition of an hard surface), different forms of coordination (e.g., tapping in-phase or in anti-phase with the event), and different sensory modalities of stimulation (e.g., auditory and visual).

For long time, intentional or not-intentional synchronization of body movements to a sound was thought a specific human's skill (Merchant and Honing, 2014). However, recently it have been discovered that animals that show vocal learning seem to be able to extract the beat and synchronize their movements to it (Patel et al., 2009; Hasegawa et al., 2011). Since both vocal learning and rhythmic synchronization depend on the solid engagement between the auditory and the motor systems to perceive and produce the movements, it has been hypothesized that the human ability to synchronize with for auditory stimuli could be a by-product of the vocal learning mechanisms that allow us to learn speech sounds and musical melodies (Patel, 2006; Patel et al., 2009).

1.4.2 Sensorimotor Synchronization Limits

Unlike animals, humans show large flexibility to synchronize to a wide range of tempi. Yet, the synchronization with a stream of paced auditory stimuli (e.g., metronome) is possible only within a certain range of interonset intervals (IOIs). The rate limits for SMS are of theoretical interest mainly because they reveal general constraints on temporal processing.

The lower IOI limit for 1:1 in-phase synchronization tends to be set by maximum frequency at which the effector can move. For finger tapping, that is typically 5-7/sec corresponding to intertap interval of 150-200 ms (Keele and Hawkins, 1982). Up to that limit, the task presents no difficulties, at least for partecipants with musical training. For musicians, that synchronization threshold lies tipically at 100-120 ms (Repp, 2003). Below that limit, taps and click usually drift apart, with subjects enabled to perceive whether are in synchrony or less.

There is also an upper IOI limit for 1:1 in-phase coordination, although it is less sharply defined. When metronome IOIs exceed about 1.8 s, a prediction of the next click becomes increasingly, and the responses begin to lag behind their respective target events, with the action becoming a pure reaction to a stimulus (Miyake et al., 2004).

The lower and upper IOI limits for SMS may represent perceptual temporal integration windows of different duration. The lower IOI limit is somewhat shorter than 160- to 170-ms duration of an auditory integration window estimated by Yabe and colleagues (1997, 1998) in studies of mismatch negativity component, a kind of evoked brain potential, reflecting the automatic detection of sound change (Yabe et al., 1997; 1998).

When the sound fall within the integration window, sequence of tones are perceived as a tightly bound group, rather than as separate events. To mention is that musicians have particularly contracted integration windows allowing optimal temporal resolution of sound events. The upper IOI limit of about 1.8 s has been related to the duration of the subjective present and the temporal capacity of working memory (Wittmann and Pöppel, 1997).

1.4.3 Development, Enhancement, and its Impairment

SMS ability takes years to develop. A study by Provasi and Bobin-Bègue (2003) showed that young children are not able to anticipate and adjust their motor responses to a metronome or musical beat until they are at least 4 years old (Provasi and Bobin-Bègue, 2003). Conversely, McAuley and colleagues (2006), in a study principally investigating changes in preferred selfpaced movements' tempo across the life span (ages 4-95), revealed that 4- and 5-year-olds did not synchronize well, if at all, whereas 6- and 7-year-olds performed much better, almost at the adult level. In addition, it was shown that elderly participants retained good synchronization ability (McAuley et al., 2006). These last results confirmed those obtained by Turgeon and colleagues (2011) that pointed towards intact timing error processing up to an advanced age (Turgeon et al., 2011).

As reported by Repp (2013), Van Noorden and De Bruyn (2009) performed an developmental SMS study in which children, ranging in age from 3 to 11 years, after listening to a familiar music played at five different tempi and, and watching an animated figure demonstrating the task of synchronizing with the musical beat by tapping with a stick on a drum, continued the task. The youngest children usually tapped at a rate of 2 Hz and did not adapt to the tempo of the music; conversely, an increasing adaptation to the tempo of beat of the music was evident from 5 years and up, with the synchronization performance that improved especially between 3 and 7 years.

The authors interpreted their results in terms of the resonance theory of van Noorden and Moelants (1999), suggesting that young children have a narrow resonance curve centered near 2 Hz, which enables them to synchronize only at their preferred tempo. The resonance curve broadened with increasing age, especially toward lower frequencies (Repp and Su, 2013).

Generally, among adults, the variability (expressed as standard deviation of the time asynchrony between the movement and the auditory stimulus; SDasy) for highly trained musicians is lower than for nonmusicians (Repp, 2010; Repp and Doggett, 2007). In another study by Fujii and colleagues (2011) where the synchronization skills were measured on professional percussionists, in which being in time is much more cogent than for other elite populations, a mean SDasy of about 16 ms when the metronome IOI was 1.000 ms, and an SDasy of about 10 ms when the IOI was 500 ms was found (Fujii et al., 2011).

Previously, Krause and colleagues (2010), studying a population of trained musicians, showed that synchronization variability was influenced by musical expertise as well as the type of specialized musical instrument. In this study was reported that synchronization variability was lowest in drummers, and lower in professional pianists than in amateur pianists, singers, and nonmusicians (Krause et al., 2010).

Individuals with motor disorders have been found to be impaired in rhythm tasks, including SMS. For example, it is found that children with developmental coordination disorder, when tapping with their left index and right middle fingers in an alternating pattern at different IOIs (IOI = 313-1.250 ms) were more variable than a control group of normally developing children, in particular for the lowest frequency (Whitall et al., 2008). The authors suggested that children with developmental coordination disorder are deficient in their auditory–motor coupling.

A few seemingly quite different disorders also lead to impaired SMS performance. For example, 7- to 11-year-old children with speech/ language impairments were found to be impaired in a range of measures of paced rhythmic tapping, but were not equally impaired in tapping in an unpaced control condition requiring an internally-generated rhythm (Corriveau and Goswami, 2009). Likewise, dyslexic adults showed higher variability than did controls when tapping in synchrony with a metronome at three tempi (Thomson et al., 2006). Impaired speech/language ability and impaired SMS might both be associated with cerebellar dysfunctions (Nicolson and Fawcett, 2011).

These findings seem to indicate cerebellar dysfunction and deficiency of cortical-subcortical networks and/or in auditory-motor coupling for the SMS impairment (Repp and Su, 2013).

1.5 Timing

"Timing" is a general term used from laypeople and scientists in different ways to refer to whether an event happens before or after some temporal landmark (temporal order judgment), but also how long an it lasts (estimation of duration), or when an it is likely to happen (prediction of event onset or offset; Coull et al., 2011).

On the one hand, temporal order judgments require an ordinal representation of time, in which the relative timing of at least two events are compared with one another in a much more categorical manner. On the other hand, estimation of duration and temporal prediction require a metrical representation of time, in which the timing (duration or onset) of a single event can be measured on a continuous, parametric timescale (Coull et al., 2011).

1.5.1 Implicit Timing

Implicit timing is a form of timing recruited for temporal predictions when the rhythmic or constant temporal dynamics of stimuli or motor responses (exogenous cues) can be used for the achievement of non-temporal tasks goals (Coull et al., 2011). In a baseball game, for example, the velocity parameters of an oncoming ball can be used by the player to estimate when it would be likely to reach him/her (time to contact); so he/she can intercept and properly struck the ball. Here, temporal predictions are used to accomplish a non-temporal goal (properly striking the ball) rather than being used to provide overt estimates of elapsing time (e.g., comparing whether time of contact for the occurring ball is shorter or longer than that of the previous ball).

Temporal predictions can be induced not only by exogenous cues, but may be stimulated voluntarily by informative warning signals (endogenous cues). For example, predicting when an amber traffic light will turn red accesses ingrained associations between sensory cues and event timing, allowing temporal predictions to be made and driving behavior to be adjusted accordingly (Coull and Nobre, 1998).

1.5.2 Explicit timing

Explicit timing demands an intentional estimate of the duration of a stimulus or an inter-stimulus interval (ISI), both in the form of perceptive discrimination (perceptual timing), where typically the individuals estimate whether the duration of one stimulus or ISI is shorter or longer than another, or in the form of a motor response (motor timing), in which subjects represent the duration of the stimulus or ISI with a repetitive, delayed, and periodic movements.

The classic widely-employed experimental paradigm for the study of motor timing is the finger tapping in a task of synchronization-continuation, introduced by Stevens (Stevens, 1886). This paradigm consists of two parts: one paced phase, in which the subject taps in synchrony with a metronome beat, and one following unpaced phase, in which the subject is instructed to continue tapping without the aid of a metronome but at the same time interval established in the paced phase.

Attraction for motor tasks like finger tapping is due to a variety of methodologically reasons. For instance, the required movements are sufficiently simple to be performed by patients with neurological disorders (O'Boyle et al., 1996, Spencer and Ivry, 2005; Schlerf et al., 2007) as well as in the constrained environments used in neuroimaging research (e.g., Desmond et al., 1997; Rao et al., 1997).

The sequence of motor responses for each phase forms a time series from which measures of accuracy and precision can be extracted, and whose patterns can be studied to infer properties of the neural timing process that was used to generate the responses.

The pacemaker–accumulator is the most cited model accounting for how temporal duration is estimated in the brain (Gibbon et al, 1984; Treisman, 1963). In this model, the raw material for time representation comes from a clock stage consisting of a pacemaker that emits pulses at a given rate, a switch controlling how the pulses are gated and an accumulator in which the number of pulses is stored during the event(s) being timed. At the onset of the sensory stimulus to be timed, the switch closes, thus allowing the pulses generated by the pacemaker to enter the accumulator. At the offset of this event, the switch opens and stops the pulse transfer. The accumulator thus achieves a monotonic integration of the pulses with the duration: the longer the stimulus duration, the more pulses are accumulated, and the longer the duration is judged to be. Temporal estimates also depend on memory and decision stages.

At the time of reward or feedback, the number of accumulated pulses can then be passed into working memory for comparison with a previously stored number of pulses. Depending on whether or not these two tallies match, the appropriate response can be given. For example, in a motor timing task the subject would withhold responding until a match is attained (Buhusi and Meck, 2005; Coull et al., 2011).

The addition of an attentional gate (Zakay, 2000) or switch (Lejeune, 2000) to the model accounts for the well-known phenomenon of "time flies when you're having fun" and, conversely, "a watched pot never boils". In this reconsidered model is supposed that brain circuits engaged by timekeeping include not only those primarily involved in time accumulation, but also those involved in the maintenance of attentional and memory resources for timing, and in the monitoring and reallocation of those resources among tasks. In brief, the less attention is paid to the passing of time since one is distracted by more absorbing events unrelated to timing, the fewer pulses are accounted for by the accumulator, leading to an overall underestimation of duration (Buhusi and Meck, 2009).

Factors influencing the attentional processes involved in timing and time perception are changes in aging, emotional arousal, and brain norepinephrine systems (Lustig and Meck, 2001; Lui et al., 2011; Penney, 1996).

This intuitive psychological model, that has been widely proved by behavioral experiments in both animals and humans has been recently challenged by neurophysiologists seeking a more neurally plausible alternative (Coull et al., 2011). Timing researchers now are increasingly convinced that the brain estimates intervals on short time scales - milliseconds to minutes and hours - in absence of a clock but with the help of a distributed network of neurons. Specifically, it is advocated that temporal processing reflect intrinsic computations based on local neural network dynamics (Goel and Buonomano, 2014).

Event-based, emergent timing and their relationship

The means by which the brain is able to estimate interval durations on millisecond time scale is not completely understood. However, two timing strategies have been identified in millisecond motor timing: event-based timing, which relies on an explicit internal representation of interval duration (Wing and Kristofferson, 1973a, b), and emergent timing, which does not appear to use such an internal representation but relies on the kinematics of movement to maintain timing (Robertson et al., 1999; Zelaznik et al., 2002; Spencer et al., 2003; Zelaznik and Rosenbaum, 2010).

There are several lines of support for the event-emergent distinction. One comes from Spencer and her colleagues (Spencer et al., 2003, 2005), who showed that patients with cerebellar damage are impaired in motor timing when performing motor tasks in which movements are repetitive and discrete (discontinuous tapping) but not when performing cyclic movements that are smooth and continuous (circle drawing). This finding supports the event-emergent framework (Harrington et al., 2004; Schlerf et al., 2007).

The second source of evidence for the event-emergent distinction is derived from studies of individual differences in timing precision. Robertson et al. (1999) showed that there were reliable individual differences within tapping tasks and within circle drawing timing tasks, but these individual differences were not correlated between these two types of tasks. The reliability of performance within each of these tasks was greater than .90, but the correlation between timing consistency in tapping and in circle drawing was not statistically significant. This result was taken to support the hypothesis that timing processes in tapping are stable and that timing processes in circle drawing also are stable, but that timing processes in tapping and in circle drawing are sufficiently different that they can be said to form different classes (Zelaznik and Rosembaum, 2010).

A third source of evidence comes from the application of the classic model of timing developed by Wing and Kristofferson (1973a, b). According to the Wing and Kristofferson model, timing variance can be ascribed to a central clock component and a more peripheral implementation component. The model predicts that series of produced time intervals should show a negative lag-one autocorrelation. Repetitive tapping tasks do indeed exhibit negative lag-one autocorrelation. On the other hand, timing tasks that use repetitive circle drawing exhibit nonnegative lag-one autocorrelation (Robertson et al., 1999; Zelaznik et al., 2008).

Different rhythmic motor tasks are used to study timing abilities. Tapping was thought to employ the event-based temporal control while circle drawing or forearm oscillations to involve emergent timing control (Robertson et al., 1999; Zelaznik et al. 2002). The discontinuous and continuous character of movements for tapping and circle drawing was considered a key factor in the engagement of one or the other timing mode (Robertson et al. 1999).

However, After Spencer and colleagues (2003) demonstrated that air finger tapping, a motor task performed in the air with no surface contact, could invoke either an event-based or an emergent timing mode, the notion that a rhythmic motor task employs only a specific timing mode for the production of rhythmic movements has been challenged. Indeed, tasks typically thought to exploit event-based timing have been shown to exhibit an emergent timing mode and vice versa. Huys and collagues (2008) showed that discontinuous slow and continuous fast tapping are considered to be two distinct topological classes. The discontinuous movements require an explicit timing (event) process to be modeled, whereas the smooth tapping movements can be modeled by a selforganized limit-cycle (emergent) process (Huys et al., 2008).

At later time, in a study by Zelaznik and Rosembaum (2010) was shown a great negative lag-one covariance in an auditory feedback circle drawing condition, suggesting that circle drawing movements, when an auditory feedback is applied, are governed by both event-based as well as emergent timing processes (Zelaznik and Rosembaum, 2010).

Finally, Studenka and colleagues (2012) showed, by inserting a tactile event into the circle drawing task, the elicitation of a timing behaviour consistent with the idea that an internal timekeeper was elicited (Studenka et al., 2012).

These evidences suggested that processes for timing are more flexible than previously thought and that the event-emergent distinction was not an all-or-none difference.

Chapter 2: Experiment I

Modulation of Isochronous Movements in a Flexible Environment: Links Between Motion and Auditory Experience

2.1 Abstract

The ability to perform isochronous movements while listening to a rhythmic auditory stimulus requires a flexible process that integrates timing information with movement. Here we explored how non temporal and temporal characteristics of an auditory stimulus (presence, interval occupancy, and tempo) affect motor performance. These characteristics were chosen on the basis of their ability to modulate the precision and accuracy of synchronized movements. Subjects have participated in sessions in which they performed sets of repeated isochronous wrist's flexion-extensions under various conditions. The conditions were chosen on the basis of the defined characteristics. Kinematic parameters were evaluated during each session and temporal parameters were analyzed. In order to study the effects of the auditory stimulus, we have minimized all other sensory information that could interfere with its perception or affect the performance of repeated isochronous movements. The present study shows that the distinct characteristics of an auditory stimulus significantly influence isochronous movements by altering their duration. Results provide evidence for an adaptable control of timing in the audio-motor coupling for isochronous movements. This flexibility would make plausible the use of different encoding strategies to adapt audio-motor coupling for specific tasks.

2.2 Introduction

The synchronization of movements to timing of external events requires a neural representation of time as a prerequisite for a rhythmic motor performance. Temporal or spatial stimuli from the external environment, which facilitate the initiation and continuation of repetitive sequential movements, have been defined as external cues (Rochester et al., 2007). A particular class of such external cues is constituted by paced auditory stimuli that range in type from a simple paced beat, such as a metronome, to specifically composed complex paced music (Wittwer et al., 2013).

The effects of different types of audio information (metronome or music) on motor rhythmic performance have been investigated both through the study of gait (Wittwer et al., 2013) and finger tapping (Repp, 1999a; Repp, 1999b; del Olmo and Cudeiro, 2005). Paced auditory stimuli for gait activities were shown to be an effective tool for gross motor rehabilitation in neurological diseases and disorders, improving spatial-temporal parameters and decreasing temporal variability of rhythmic movements in gait (Thaut et al., 1996; McIntosh et al., 1997; del Olmo and Cudeiro, 2005; del Olmo et al., 2006; Hausdorff et al., 2007; Arias and Cudeiro, 2008; de Dreu et al., 2012). On the other hand, it was shown that temporal precision of self-paced finger tapping was limited by variability in a central timekeeper and by variability in the peripheral motor system, and that internal timekeeping processes were stabilized by periodic external signals (Semjen et al., 2000).

The role of visual and tactile information in the control of movements is also well documented. It is stated that the way in which visual information is processed and used for guiding movements might depend on the specific task's requirements (Schrater and Kersten, 2000; Greenwald et al., 2005). The contribution of tactile information on the temporal control processes of rhythmic movements has been recently explored (Studenka et al., 2012), however, the influence of the visual feedback on the production of rhythmic movements is not substantially taken into account. Thus, it is difficult to establish what is the specific contribution of the auditory input to motor synchronization seeing that the contribution of visual and tactile information is far from negligible (Brochard et al., 2008; Wing et al., 2010). To our knowledge there is no task model for studying the temporal control of rhythmic movements that takes into consideration the minimization of both sensory factors.

In addition, the non temporal characteristics of an auditory stimulus (nature, energy and complexity) have a decisive influence on the perception of time (Allan, 1979). In psychophysical studies on duration discrimination, basically two types of time intervals of different natures are used: filled and empty intervals (Allan, 1979; Rammsayer, 2010). While in a filled interval a signal is presented continuously throughout the interval, in empty intervals only the onset and the offset of the interval are marked by a brief sensory event. Thus, an empty interval is a silent duration in which no signal is present during the interval itself (Rammsayer, 2010). It has been showed that duration discrimination of filled auditory intervals is significantly different from that of empty auditory intervals and that the filled intervals are perceived as longer than the empty intervals, a phenomenon called "filled duration illusion" (FDI; Craig, 1973; Adams, 1977). FDI is evident when a continuous tone is compared with a silent interval (Wearden et al., 2007), but it is also present when discrete events (sounds or movements) are inserted and subdivide a silent interval (Wohlschläger and Koch, 2000; Repp, 2008a). Equally spaced auditory subdivisions of silent intervals, approximating a musical rhythm, influence the perception and the production of rhythmic movements, with the subjects tapping at a tempo slower than the original when reproducing subdivided interonset intervals (Repp, 2008a). Moreover, the FDI effect on tempo of musical performance has been demonstrated in highly trained musicians who intended to keep the tempo constant (Repp and Bruttomesso, 2009). Although different types of filled intervals have already been used in previous psychophysical studies, a complex auditory stimulus such as music, which can be considered as a complex subdivision of a filled interval, has never been taken into account. Rhythm perception of streams of beats or tones is related to the duration of interonset intervals defined by periodic auditory markers (Repp, 2005). In music, rhythmic organization stems from interaction between groupings (i.e., hierarchical recursive structures composed by adjacent notes and meters) that are extrapolations of isochronously defined tones perceived through metrical accents (Jackendoff and Lerdahl, 2006; Large and Snyder, 2009).

Furthermore, while the mnemonic properties of visual imagery are well established, investigation of potential mnemonic properties of auditory imagery to date is limited. The introspective persistence of an auditory experience, including that constructed of components drawn from memory in absence of direct sensory instigation of experience, has been defined as auditory imagery (Hubbard, 2010; Bishop et al., 2013). The auditory imagination can be a very vivid experience and it can be surprisingly accurate, preserving many characteristics of the real auditory stimulus: pitch (Halpern, 1989), timbre (Halpern et al., 2004), and tempo (Halpern, 1988). Using neuroimaging techniques it was shown that the ability to imagine an auditory stimulus appears to vary among people (White et al., 1977), and seems to be influenced by training, or musical experience in perception, performance, and composition (Keller and Koch, 2008; Hubbard, 2010). Various works have documented the similarity of neural mechanisms in imagery and perception, but studies of auditory imagery have shown that the accuracy of tempo is affected during audio recall (Levitin and Cook, 1996).

Finally, music affects the limbic system, which is strongly implicated in processing of emotions and in controlling memory (Jäncke, 2008). The emotional content of music can possibly influence memory retrieval, however it seems impossible to avoid emotions, which likely reflect immediate personal experiences, even while listening to non musical auditory stimuli (Bradley and Lang, 2007).

On the basis of the above-mentioned findings and theories, we have developed a combined task in which sets of repeated isochronous wrist's flexion-extensions (IWFEs) are performed in one session, under seven different conditions while minimizing visual and tactile information. In accordance with the objective of studying the effects of defined audio characteristics (presence, interval occupancy, and tempo), IWFEs were recorded under the following conditions: self-paced free from auditory constrain, driven by streams of paced clicks as empty intervals, or by excerpts of paced music as complex filled intervals, and self-paced during recall of the previous auditions.

The general purpose of this work was to study how the characteristics of a paced auditory stimulus, untied from visual feedback, interact with temporal control of wrist's repetitive isochronous movements performed with no direct surface opposition, thus minimizing also tactile information. More specifically, the aims of the study were twofold: firstly, we investigated how the characteristics of auditory stimulus influence the precision of an isochronous performance, defined as performance of repeated movements having a uniform duration. Secondly, we explored whether the auditory stimulus with distinct characteristics (i.e., interval occupancy and tempo) and its recall may influence differently the accuracy of IWFEs tempi in presence and in the absence of the audio information, where auditory imagery is involved (Intons-Peterson, 1980; Hubbard, 2010). In particular, we wanted to extend the research about FDI and observe whether music had the "illusory power" possessed by filled intervals **(**Wearden et al., 2007**)** and thus capable of modulating a rhythmic performance by slowing it down due to its ability to expand the auditory image's tempo used in recall for motor performance.

2.3 Methods

Participants

A group of 78 right-handed volunteers (37 males, ages 20-27, average 24.1±2.4 years; 41 females, ages 18-27, average 23.0±2.7 years) took part in the recording sessions. All participants were naive to the purpose of the study; they were neither musically trained nor listeners of a classical music repertoire, and reported no auditory, motor, or other neurological impairments. The experimental protocol conformed to the requirements of the Federal Policy for the Protection of Human Subjects (U.S. Office of Science and Technology Policy) and of the Declaration of Helsinki, and has been approved by the Research Ethics Board of our Institution (Comitato Etico Area Vasta Centro AOUCareggi, Florence, Italy). All participants provided an informed consent in written form.

Set up

Each subject was tested individually, sitting upright on a chair with the legs comfortably positioned on leg-rest. An armrest was attached to the chair and supported the participant's right arm, whereas the forearm was placed in a relaxed horizontal position (Fig. 1A). The wrist and hand of the subject were free to move in mid-air with no direct opposition, thus minimizing tactile information. In order to reduce possible interference of visual information, the subject was requested to wear a blindfold. Environmental noise was reduced by the use of headphones (K 240 Studio, AKG Acoustics GmbH, Wien, AT), which were also used for the clean delivery of audio information. This setup was designed to minimize all information that is known to influence motor strategies (i.e., visual, tactile, and environmental noise) and that may result in a different motor performance (Bove et al., 2009; Saijo and Gomi, 2010). A triaxial accelerometer (ADXL330, Analog Devices Inc., Norwood, MA 02062) was placed on the dorsal aspect of the hand, over the proximal part of the 2nd-3rd metacarpal bones. The sensor, placed in a small pocket, was kept in position by an elastic band and secured by a Velcro strap. Sensor output was acquired and digitized at 200 Hz through PCI-6071E (12-Bit E Series Multifunction DAQ, National Instruments, Austin, TX, USA).

Audio Stimuli

Audio stimuli were paced streams of clicks and excerpts of music. Music excerpts of 60s duration were extracted from original professional productions. Selection of music fragments was made on the basis of having a simple and explicit rhythmic structure and a stable tempo that remained constant throughout time. Music fragments were taken from a variety of musical styles popular among young people: rock, techno, dance, trance, hard rock, and film music. Since it is known that the determination of perceptual musical tempo can be ambiguous (Mc Kinney and Moelants, 2007) and that algorithms for music tempo extraction have several limitations (McKinney et al., 2007), three musical experts (professionals with musical experience) were asked to verify independently the tempo of the excerpts. The purpose was to be as accurate and sure as possible in the choice of unambiguous paced music excerpts. Only fragments for which the experts collectively agreed of having a single musical tempo were selected.

All chosen fragments had small tempo variations due to live performance. Therefore, the tempo for each fragment was analyzed, beat-mapped, and set to fixed beats per minute (bpm, used as a measure of tempo in music) using the softwares Jackson (http://vanaeken.com/; accuracy is within a 0.001 bpm margin) and Audition (Adobe Systems Inc., San Jose, CA 95110-2704, USA).

Our time manipulations were all well below 5% deviation of the mean music tempo (professional performances have minimal deviations from mean tempo; Dannenberg and Mohan, 2011) and thus below the detection threshold for temporal changes in music (Ellis, 1991; Madison and Paulin, 2010). We didn't use fragments likely to be familiar to the listeners since it has been shown that high familiarity with a song installs an accurate long-term memory of its tempo (Levitin and Cook, 1996; Quinn and Watt, 2006). Streams of clicks of 60 s duration were produced using the audio editor Audacity (GNU/GPL, http://audacity.sourceforge.net/), via the Generate Click Track function. The duration of an individual click was set to10 ms, and the click sound was set to white noise. The music and clicks stimuli were set to fourteen reference tempi ranging from 64 to 176 bpm (1.067 to 2.933 Hz, Table 1). The same fourteen tempi were chosen for both streams of clicks and excerpts of music. Audio files were all normalized to -0.3 dB as the highest peak and stored as waveform (waveform audio file; 44.1 kHz; 16-bit depth) using Audition. Fade in and fade out (10 ms) were placed at the beginning and end of each file. Audio stimuli were presented binaurally to the subjects through headphones (Fig. 1B).

Data format

Subjects were asked to perform sets of IWFEs (blue arrows in Fig. 1A) and kinematic parameters were evaluated. Data from the sensor were stored and an off-line analysis was implemented. Raw data from the triaxial accelerometer were elaborated to extract wrist's flexion-extension. The signal extracted from the accelerometer presented a minimum when the wrist reached the maximum flexion and a maximum when it reached the maximum extension. The duration of a single wrist's flexion-extension (i.e., IWFE duration) was calculated as the difference between two consecutive flexion-extension minima (red double headed arrow and marks in Fig. 1C) using a custom software developed in Matlab®. To avoid initial and final transients, the first and last 5 seconds of each recording were excluded from analysis (Repp, 2005; Repp, 2011a). Considering that tempi of the recorded IWFEs sets were extremely variable, giving rise to a quantitative redundancy of tempi obtained in overall, we have decided to rank them as ranges (Table 1). IWFEs sets were then assigned to a defined range according to their tempo.

Session

Each subject had participated in one session in which he/she performed 15 sets of repeated IWFEs under various conditions. A single session (Fig. 1D) was comprised of a baseline recording (3 sets) and 2 blocks (12 sets). The auditory stimulus used for each block had a defined tempo, which was different between blocks. A block was comprised of the performance of 6 sets, each under a different condition. Overall, in a single session the performance of the IWFEs sets was executed under seven conditions: in absence of auditory information (free, Fr), while listening to a stream of clicks (Cl), after 2 and 5 minutes from the end of the Cl condition (Cl2 and Cl5, respectively), while listening to an excerpt of music (Mu), after 2 and 5 minutes from the end of the Mu condition (Mu2 and Mu5, respectively). Sets of IWFEs were recorded in all conditions. The order in which the clicks or music stimuli were presented was set to obtain equivalent number of subjects that received first one or the other.

The subject was instructed to restrain from listening to music during the day of the session. Each session began with instructions on how the sets of wrist's flexion-extensions were to be performed, followed by a short practice test. During the practice test, IWFEs were recorded and evaluated to assess whether the instructions were understood; after the practice test, the subject was asked if he/she felt comfortable with the task. Recordings from the practice test were not used for further analyses. The session started with recording in the Fr condition, which consisted of three IWFEs sets. In the first set, the subject was asked to perform IWFEs in a self-paced manner (first recording in Fr condition). In the second and third sets, the subject was asked to perform IWFEs faster and slower (respectively) than those of the first set (second and third Fr recording). The subject was then instructed to perform a set of repetitive IWFEs while listening to clicks or music at a similar pace concurrently with the tempo of the delivered audio (i.e., maintaining an in-phase 1:1 relationship between repeated wrist's flexion-extensions and the tempo of the audio, conditions Cl or Mu). Then, instructions to subject for IWFEs performances in recalls were of the kind: "now, try to hear in your head the auditory stimulus just heard" (immediately after the end of the stimulus, see Zatorre and Halpern, 2005). After a 2 min break, the subject was asked to perform IWFEs as accurately as possible at the tempo of the auditory stimulus just heard while concurrently hearing mentally the stimulus itself (conditions Cl2 or Mu2). Then, subjects received the instruction: "try again to hear in your head the auditory stimulus". After a supplemental 2 min break, the subject was asked to perform again another set of repetitive IWFEs while concurrently hearing mentally the stimulus (conditions Cl5 or Mu5). The session continued with the recordings of IWFEs in a reversed order (i.e., with the Mu conditions if Cl was recorded first, or vice versa). In order to obtain a balanced number of performances for the fourteen chosen reference tempi, the two tempi that were selected for the blocks were randomized for each single session.

Statistical methods

The data were studied and the results described using different statistical approaches depending on the purpose of the specific analysis (Sarter and Fritschy, 2008). In order to evaluate the precision and accuracy of IWFEs, we used descriptive statistics such as averages, standard deviations (SDs), and coefficients of variation (CVs = SD / average × 100). The Pearson product-moment correlation coefficient (r), which is a measure of the correlation between two variables, was used to measure the strength of the linear association between the average IWFEs durations and their SDs. CVs of IWFEs durations were used to investigate whether the characteristics of an auditory stimulus influence the precision of IWFEs performance. If not indicated otherwise, CVs of IWFEs and

IWFEs durations are to be considered as the condition's and the set's averages, respectively. In order to explore whether the characteristics of the auditory stimulus influence differently the accuracy of IWFEs tempi in audio and recall conditions, percent differences between the tempo of the IWFEs set performed (number of IWFEs per minute) and the reference tempo have been calculated and averaged per ranges as**:** (performed tempo - reference tempo) / reference tempo × 100. This calculation was repeated per condition (i.e., audio and recall). One way ANOVA was used to evaluate within-condition differences of CVs of the IWFEs durations. ANOVA analyses were followed by Bonferroni post-hoc tests to confirm the significance of the differences between conditions. Finally, a three-way ANOVA analysis was used to analyze the influence of clicks or music on percent differences of the tempi of the IWFEs sets in audio and the recall conditions. Also the three-way ANOVA analysis was followed by post-hoc tests. For each subject, only data of the first block were used in this latter analysis. All ANOVA based differences were considered statistically significant when $p < 0.05$.

2.4 Results

The dataset

We have recorded a total of about 1000 sets of IWFEs. For each set, we first calculated within-set averages and SDs of IWFEs durations; sets whose CV was >6% (6% was set as the maximum acceptable CV value for data dispersion) were excluded from further analysis. Using this criterion, less than 7% of the IWFEs sets were eliminated. Isolated sets in which the subjects have performed IWFEs to a tempo different from that of the audio sample (i.e., movements performed at half or double tempo of the auditory stimulus; Van Noorden and Moelants, 1999; Moelants, 2002) were also excluded. Each within-set average of the IWFEs tempi received a rank in reference to the fourteen ranges of tempi while considering the condition under which it was recorded (Table 1). Sets with IWFEs tempi below 1.017 Hz and above 3.000 Hz, mainly pertaining to the Fr condition, were excluded from analysis. Our final dataset consisted of 912 sets (n=126 for condition Fr, n=145 for Cl, n=125 for Cl2, n=126 for Cl5, n=138 for Mu, n=129 for Mu2, and n=123 for Mu5) distributed over the 78 subjects, each containing a relatively high number of IWFEs (averaging from 86.63, for condition Mu5, to 93.22, for condition Cl5). ANOVA analyses on an equal number of sets per condition were performed (n=10 at 1.067 Hz, n=7 at 1.200 Hz, n=7 at 1.333 Hz, n=7 at 1.467 Hz, n=8 at 1.600 Hz, n=9 at 1.733 Hz, n=10 at 1.867 Hz, n=9 at 2.000 Hz, n=8 at 2.133, Hz, n=9 at 2.267, Hz, n=10 at 2.400, Hz, n=7 at 2.533, Hz, n=9 at 2.700 Hz, n=7 at 2.933 Hz). In our analyses no differences were seen in comparisons of gender, therefore, data from females and males were pooled together.

The precision of IWFEs performance

First, when we explored whether the tempo characteristic of the auditory stimulus influenced the variability of IWFEs performance, we observed a clear correlation between IWFEs durations and their SDs when sets were compared for condition and for the fourteen ranges of tempi (separately). As expected, slower movements had greater variability in terms of duration than faster movements (Semjen et al., 2000; Rodger and Craig, 2011; Lorås et al., 2012). This is shown in Figure 2A, B, C where the average within-ranges SDs for the seven conditions are represented as a function of the average within-ranges durations of IWFEs. In all conditions, the correlation coefficients of SDs versus IWFEs durations, calculated for the fourteen ranges, were similar (Table 2).

To investigate if, and to what extent, the presence and interval occupancy characteristics of the auditory stimulus influence the precision of the isochronous performance, we compared the within-condition CVs of IWFEs durations among the seven conditions. CVs values ranged from 4.49±0.27 (within-condition CVs values ± within-condition SDs), for the Cl condition, to 4.90±0.26, for the Mu2 condition (Fig. 2D). One-way ANOVA analysis of CVs (factor = condition), performed on Fr, Cl, and Mu, demonstrated no significant differences among the three conditions ($F_{2,309} = 2.658$, $p > 0.05$) and, consequently, listening to clicks or to music did not influence the precision of the isochronous performance. Since no significant differences were seen among Fr, Cl and Mu, the Fr condition was omitted from further analysis. ANOVA analyses were then performed to compare the audio conditions with the two own recall conditions. ANOVA performed on Cl, Cl2, and Cl5 ($F_{2,309} = 15.353$, $p < 0.001$) or Mu, Mu2, and Mu5 ($F_{2,309} = 3.358$, $p < 0.05$), revealed highly significant and significant differences among conditions, respectively. The post-hoc comparisons among pairs provided highly significant differences between the auditory and the recall conditions (Cl vs. Cl2, Cl vs. Cl5, Mu vs. Mu2, and Mu vs. Mu5, $p < 0.001$), whereas not significant differences were found between recall conditions (Cl2 vs. Cl5 and Mu2 vs. Mu5, $p > 0.05$).

The accuracy of IWFEs tempi during recall

In recall conditions, subjects performed the sets of IWFEs at a tempo different from that performed in the previous listening condition. To study whether or not listening to clicks or to music influence differently the accuracy of IWFEs tempi in audio conditions and during recalls, we calculated the percent differences between the tempo of IWFEs set obtained in the audio or in the recall conditions and the reference tempo of the auditory stimulus. While percent differences of tempi of the IWFEs sets in the Cl and Mu conditions were very close to the tempo of audio stimuli (±0.2%), percent differences of tempi were evident in IWFEs sets performed 2 min after the listening of audio and persisted in those performed 5 min after. Percent differences of tempi for all recall conditions, as a function of ranges in Hz, are shown in Figure 3. Percent differences of tempi extended from about 13.6% in Cl2 (from -6.35±4.93%, range 1.067 Hz, to

7.27±4.69%, range 2.933 Hz) to about 15.3% in Cl5 (from -6.33±5.61%, range 1.067 Hz, to 8.94±2.03%, range 1.467 Hz). Percent differences of tempi in Mu2 were about 16% (from -13.47±2.69%, range 2.533 Hz, to 2.45±3.24%, range 1.6 Hz) and in Mu5 were about 18.2% (from -16.04±3.38%, range 2.7 Hz, to 2.19±2.45%, range 1.6 Hz).

A three-way ANOVA was performed on the six conditions Cl, Cl2, Cl5, Mu, Mu2, and Mu5 for the stimulus (Cl or Mu; factor 1), time (t0 = Cl or Mu; t1 = Cl2 or Mu2; t2 = Cl5 or Mu5; factor 2) and tempo (the fourteen ranges of tempi; factor 3). ANOVA analysis demonstrated highly significant differences for the stimulus ($F_{1,384} = 224.303$, $p < 0.001$), for the time ($F_{2,384} = 24.352$, $p < 0.001$), and for the tempo ($F_{13,384} = 4.722$, $p < 0.001$). The interactions between the stimulus and the time or the stimulus and the tempo showed highly significant p values ($F_{2,384} = 47.753$, $p < 0.001$ and $F_{13,384} = 7.214$, $p < 0.001$, respectively), while that between the time and the tempo gave not significant p value ($F_{26,384} = 1.315$, $p > 0.05$). The interaction among the stimulus, the time and the tempo was found highly significant ($F_{26,384} = 2.132$, $p < 0.001$).

Post-hoc comparisons for the time factor showed highly significant differences between the audio and the two recall conditions (both comparisons, $p < 0.001$) and no significant difference between the two recall conditions ($p > 0.05$). More specifically, post-hoc comparisons among groups of factor 1 (stimulus) within each factor 2 (time) level gave no significant differences between Cl and Cl2 ($p > 0.05$), Cl and Cl5 ($p > 0.05$) or Cl2 and Cl5 ($p > 0.05$), whereas highly significant differences were found between Mu and Mu2 ($p < 0.001$) or Mu and Mu5 ($p < 0.001$). The comparison between Mu2 and Mu5 gave no significant differences ($p > 0.05$). Our analysis shows that only the music recall conditions result in performances of IWFEs at tempi that are significantly different from those performed while listening to the original audio. In addition, post-hoc comparisons among groups of factor 2 (time) within each factor 1 (stimulus) level gave highly significant differences between Cl2 and Mu2 ($p < 0.001$) or Cl5 and Mu5 ($p < 0.001$), whereas no significant differences were found between Cl and Mu ($p > 0.05$). These last results indicate highly significant differences between the Cl recalls and the Mu recalls of the same time level but not significant differences between the audio conditions. Altogether our data indicate that subjects, in recall conditions, tend to perform IWFEs at slower tempi after listening to music than after listening to clicks; this is particularly evident at the high ranges of tempi (see Fig. 3).

2.5 Discussion

The tempo characteristic of the auditory stimulus influences the variability of performance in terms of duration as the SDs are greater for longer IWFEs durations. IWFEs durations and their SDs are clearly correlated and this correlation remains constant in the free, the audio and the recall conditions. In addition, when performances are compared among conditions, it is evident that the presence and the interval occupancy characteristics do not modify the precision of the performance when confronted with the baseline recording (Fr). The precision of the IWFEs performance globally decreases during the recall of an audio stimulus. This is demonstrated by a significant increase of CVs when subjects perform IWFEs while remembering the audio previously listened to. Finally, in the absence of an auditory input (i.e., in recall condition), previously listened music and clicks affect differently the accuracy of performances by influencing the tempo of the IWFEs sets.

Experiment construction

Our study is based specifically on the integration of an auditory input with motion and the experiment is designed to minimize possible interferences by other sensory modalities. In addition, the inclusion of a condition in which IWFEs are performed in silence (the Fr condition), not associated to previous synchronization, represents a concrete reference point for the study of the other conditions where auditory-motor or recall-motor integrations are requested. Although the possibility exists that different subjects may variously interpret the Fr condition, what remains unambiguous is the fact that there could be no cases for which integration might occur with auditory input or with recall of previous synchronization. Also, the inclusion of a condition where IWFEs are performed while listening to music is further motivated as the need to extend models limited by the discrimination of simple first-order stimuli, based only on duration, that are unlikely to represent biological mechanisms underlying temporal processing (Mauk and Buonomano, 2004; Saijo and Gomi, 2010). Finally, differences regarding the perception of music (Fujioka et al., 2004; Fujioka et al., 2005), the vividness of auditory images and the potency of their effects on skilled behavior that were observed in musically trained individuals (Aleman et al., 2000; Brodsky et al., 2003; Highben and Palmer, 2004; Herholz et al., 2008), represented the reasons for us to study a homogenous group constituted by only musically untrained subjects.

Precision of the isochronous performance

Our data showed that when both tactile and visual information are minimized, the listening alone to paced auditory stimuli (clicks or music) does not improve the precision of an isochronous performance. This is of importance given the emphasis present in literature regarding the ability of an auditory stimulus to drive and facilitate rhythmic motor behavior (Zatorre et al., 2007), and regarding the close relationship of body movements to beat and rhythm patterns of the musical audio stream (Leman, 2007; Burger et al., 2013). In particular it has been proposed that music influences corporeal articulations through synchronization, as synchronizing to a beat is easy and spontaneous (Leman, 2007). Although neither in favor nor against the concepts linking music (or, more broadly, paced audio) perception to body movement, our data suggest that even if music "makes us move", the precision of motor performance is not improved, at least in terms of isochrony.

Moreover, it is known that sensitivity to time discrimination is much higher when intervals are marked by auditory rather than by visual signals (Grondin, 2010). Tapping tasks have demonstrated less temporal variability when rhythmic movements were marked by auditory than visual stimuli (Zarco et al., 2009). The paced auditory stimuli facilitate synchronization with respect to paced visual stimuli as shown in a recent study by Lorås and colleagues (2012) in which tapping with auditory and visual (flashing) metronomes were compared. On the other hand, it was shown how sensitivity to time discrimination is much lower when temporal intervals are marked by input from only one modality, either auditory or visual (Grondin, 2010). Studenka and colleagues (2012) asked subjects to perform repetitive rhythmic movements in a tapping task both in the presence and in absence of tactile information. It was shown that no-tactile feedback tapping had a significantly larger coefficient of variation of movement durations than tactile feedback tapping (5.6% and 4.5%, respectively), indicating that the removal of tactile feedback increases temporal variability of rhythmic movements. In addition, when comparing the above findings (from no-tactile feedback tapping) with our data, it is easy to observe that CVs values of movement durations are higher when visual information is present, as in the Studenka (2012) procedure, and lower where visual information is minimized, as in our conditions (interestingly 5.6% vs. 4.49% to 4.90%, respectively). Although it is difficult to compare data from different experimental models, it is possible to hypothesize that in a synchronization motor task where tactile information is minimized, the presence of visual information results in a disadvantageous audio-motor interaction and thus in weakened coupling of movement with auditory information. Audio-visual integration is thought to help us in the perception of information, allowing us to focus on relevant information and filter out irrelevant information, yet it may cause distractions when our attention is captured against our will by information that is irrelevant for our task (Koelewijn et al., 2010).

Accuracy of the isochronous performance

It is well established that auditory imagery refers to the aspect of auditory cognition in which auditory information is internally generated and processed in the absence of real sound perception (Herholz et al., 2012). The different audio components of the auditory imagery are differently preserved, as the temporal component of auditory images is considerably less precise than components related to pitch (Janata and Paroo, 2006). Also, the characteristics of an auditory input influence extensively the properties of the temporal components in auditory images (Janata and Paroo, 2006).

In our paradigm of audio-motor and recall-motor integration the interval occupancy and the tempo characteristics of auditory stimulus become influential only during recall, where auditory imagery is implicated, for a comprehensive feature of rhythmic motor performance: the tempo. Subjects, in recall conditions, performed the sets of IWFEs at slower tempi after listening to music than those performed after listening to clicks, thus demonstrating that music, a complex audio information, has the "illusory power" of the filled interval (Wearden et al., 2007) and is thus capable of modulating, by slowing it down, a rhythmic motor performance. In addition, although one could expect that, due to difficulty in coordination, the tempo of the performance would tend to diminish in individuals non-musically trained at faster tempi (Repp and Bruttomesso, 2009), we observed paradoxical faster performances at these tempi (from 2.533 to 2.933 Hz) during the recall of clicks. Therefore it is possible to infer that the interval occupancy of an auditory input might result in contractions or expansions of the auditory image's tempo used for a rhythmic motor performance. This is more evident at the high ranges of tempi (see Fig. 3) where there is a clear trend to perform movements at faster or slower tempi after the listening of clicks or music, respectively.

Tempo is represented within auditory images that emerge as activities of several brain areas (Halpern, 1988; Hubbard, 2010). The complexity of audio information is a crucial factor in modulating the activity of many rhythms related to cortical regions, and the organization of music into meaningful time patterns puts load on memory (Bengtsson et al., 2009). Thus, we can hypothesize that in order to handle timing of musical images we anticipate the load of processing by allocating more time and then, consequently, slowing the tempo. Conversely, in order to handle timing for images of clicks we anticipate a rapid process, allocate less time, and consequently perform movements at faster tempi. If this allocation has a fixed time value (in the range of a few dozen milliseconds), its effect could be unmasked at the high ranges of tempi, as we observed.

Little attention has been paid to the role of imagery in music performance. Auditory imagery is often exploited by musicians in a variety of situations (i.e., practice, rehearsal, etc.) in order to enhance different aspects of performance. Musicians use the auditory imagery of note and rhythm patterns to build consistency, note accuracy, and a musical understanding, but overall to achieve ideal sound during the performance (Trusheim, 1993; Keller, 2012). It was reported that auditory imagery may assist in selecting the sequential order in which to strike piano keys (Keller and Koch, 2006a); it promotes an efficient (rapid) movement by enabling thorough action preplanning (Keller and Koch, 2008); it allows for economical force control by reducing the performer's reliance on tactile feedback (Keller et al., 2010); and finally, it was shown that it facilitates timing accuracy by optimizing movement kinematics (Keller and Koch, 2006). Hence, although the mental experience of auditory features of sounds during performance was shown to be effortful but justifiable when artistic perfection is the goal (Keller, 2012), our data show that in musically untrained subjects the auditory imagery does not favor a rhythmic motor performance in terms of precision and accuracy. In addition, the tempo of an isochronous performance, executed while recalling an auditory stimulus, deviates much more from the tempo of auditory stimulus previously listened when the latter is complex. These findings are of relevance in order to get insights on the mnemonic properties of auditory imagery that are still poorly investigated (Hubbard, 2010).

2.6 Conclusions

Our results provide experimental evidence for an adaptable control of the audio-motor coupling for isochronous movements encompassing cognitive and dynamic systems frameworks. Seeing that timing processes are sensitive to the characteristics of an auditory stimulus, it would make plausible the use of different encoding strategies to adapt audio-motor coupling for specific tasks, as also recent data seem to suggest (Cicchini et al., 2012). Finger tapping in synchrony with an external auditory stimulus, often a paced metronome but also music albeit rarely, remains a popular paradigm due to its simplicity and long history. The basic principles revealed by finger tapping studies can be applied to other forms of synchronized movements, especially if they involve periodic contacts with a surface as in the case of gait (del Olmo et al., 2006). Seeing that the arms move more freely than the lower limbs during walking, our experimental model, characterized by a rhythmic motor activity such as the rhythmic oscillations of the wrist in which tactile information is kept to a minimum, could be a way to gain basic information about "non-goal directed" rhythmic movements such as arm swing. To study how paced auditory stimuli interact with the temporal control of isochronous movements untied from visual feedback and with no direct surface opposition allows for novel and potentially fruitful non-invasive exploration of time-related cognitive abilities of the human brain.

Chapter 3: Experiment II

Music, clicks, and their imaginations favor differently the event-based timing component for rhythmic movements

3.1 Abstract

The involvement or noninvolment of a clock-like neural process, an effector-independent representation of the time intervals to produce, is described as the essential difference between event-based and emergent timing. In the Experiment I we studied repetitive IWFEs, performed while minimizing visual and tactile information, to clarify whether non-temporal and temporal characteristics of paced auditory stimuli affect the precision and accuracy of the rhythmic motor performance. Here, with the inclusion of new recordings, we expand the examination of the dataset described in our previous study to investigate whether simple and complex paced auditory stimuli (clicks and music) and their imaginations influence in a different way the timing mechanisms for repetitive IWFEs. Sets of IWFEs were analyzed by the windowed (lag one) autocorrelation - $w\gamma(1)$ -, a statistical method recently introduced for the distinction between event-based and emergent timing. Our findings provide evidence that paced auditory information and its imagination favor the engagement of a clock-like neural process, and specifically that music, unlike clicks, lacks the power to elicit event-based timing, not counteracting the natural shift of $w\gamma(1)$ toward positive values as frequency of movements increase.

3.2 Introduction

In a previous work, we studied repetitive IWFEs to clarify whether non-temporal and temporal characteristics of paced auditory stimuli affect rhythmic motor performance. Results showed that the distinct characteristics of an auditory stimulus influenced differently the accuracy of isochronous movements by altering their duration and provided evidence for an adaptable control of timing in the audio-motor coupling for isochronous movements (Bravi et al., 2014a). With the present work we seek to analyze whether paced auditory stimuli with distinct characteristics and their recall influence timing mechanisms for repetitive IWFEs.

The involvement or noninvolment of a clock-like neural process, an abstract effector-independent representation of the time intervals to produce (Wing and Kristofferson, 1973a, b), is described as the essential difference between event-based and emergent timing, i.e., the two forms of timing for the control of rhythmic movements (Spencer and Ivry, 2005; Baer et al., 2013). Event-based timing, stemming from the information processing theory, is nicely captured by the two-level model proposed by Wing and Kristofferson showing that temporal precision in self-paced tapping is determined by variability in a central timekeeper and by variability arising in the peripheral motor system (Semjen et al., 2000). Emergent timing, deriving from the dynamics systems theory, is considered to arise from dynamic control of non-temporal movements parameters (Schöner, 2002; Huys et al., 2008) such as stiffness playing a major role for regulating movement frequency (Turvey, 1977; Delignières et al., 2004). In particular, event-based timing predicts that a longer interval should be followed by a shorter interval and viceversa. A statistical approach that is used for identifying the timing mode of a rhythmic activity is the (lag one) autocorrelation $\gamma(1)$ that returns negative values (between -0.5 and 0), when event-based timing controls the timed movements, or positive values (between 0 and 0.5), in case of involvement of emergent timing (Wing and Kristofferson, 1973a,b). Extensions of the two-level model for synchronization have been examined (Vorberg and Wing, 1996; Pressing, 1998; Vorberg and Schulze, 2002) and the available models of synchronization, based on a timekeeper estimating time integrated with information on previous performance and on expected events (Joiner and Shelhamer, 2009), have been recently evaluated for their predictive abilities (Jacoby and Repp, 2012).

Different rhythmic motor tasks are used to study timing abilities. Tapping is thought to employ the event-based temporal control while circle drawing or forearm oscillations involve emergent timing control (Zelaznik et al., 2002). Robertson and colleagues (1999) found that temporal precision in tapping was not related to temporal precision in circle drawing and hypothesized that the two tasks involved distinct timing processes, the former favoring a process of timing "with a timer" and the latter a process of timing "without a timer". The discontinuous and continuous character of movements for tapping and circle drawing was considered a key factor in the engagement of one or the other timing mode (Robertson et al., 1999). Theoretical analyses (Schöner, 2002; Huys et al., 2008) substantiated that the class of discontinuous movements, defined as having a definite beginning and end, favors the involvement of clock-like neural processes.

The discreteness in rhythmic movements is not the only variable favoring the utilization of event-based timing. Recent studies have demonstrated that salient auditory markers, i.e., streams of clicks and tactile feedback, are also able to elicit the event-based timing (Torre and Delignières, 2008; Studenka et al., 2012). Also, it is known that the characteristics of an auditory stimulus, and particularly non-temporal characteristics such as nature, energy and complexity, have a decisive influence on the perception of time (Allan, 1979). In fact, the framework for synchronizing movement to different classes of auditory stimuli such as streams of clicks or music may be very different. Paced clicks are simple and brief sensory events marking only the onset and the offset of empty silent intervals. A signal consisting of a stream of clicks provides unique informational economy by making the next click in the sequence perfectly predictable (Fraisse, 1982). Rhythm perception in this case is simply related to duration of the interonset interval as defined by periodic auditory markers (Repp, 2005). Conversely, paced music consists of a complex sound architecture filling entirely temporal intervals subdivided by periodic pulses. Musical beat perception is a brain function involving the extraction of a periodic pulse from spectro-temporally complex sound sequences as hierarchical recursive structures composed by adjacent notes and meters, allowing the listener to infer a steady succession of beats (Jackendoff and Lerdahl, 2006; Large and Snyder, 2009; Patel and Iversen, 2014). Finally, also movements participate to beat perception in music encoding, even for ambiguous musical rhythm (Phillips-Silver and Trainor, 2007). These results suggest that movement takes part in the coding of rhythm from audition.

People are able to mentally represent an auditory stimulus and retain it (Halpern, 1992). The introspective persistence of an auditory experience, including that constructed of components drawn from memory, in the absence of direct sensory instigation of experience, has been defined as auditory imagery (Hubbard, 2010; Bishop et al., 2013). Zelaznik and Rosenbaum (2010) reasoned on the fact that kinematic differences in tapping and circle drawing may not satisfy entirely for the distinction between event-based and emergent timing and on whether sensory representation of movement may be significant for the difference between the two timing conditions. The authors, using a paradigm of correlation for individual differences between timing variability in tapping and circle drawing, showed that the distinction between event-based and emergent timing resides also in the representation of the goal and provided evidence that the auditory representation of movement favors the event-based timing (Zelaznik and Rosenbaum, 2010).

After Spencer and colleagues (2003) demonstrated that air finger tapping, a motor task performed in the air with no surface contact, could invoke either an event-based or an emergent timing mode, the notion that a rhythmic motor task employs only a specific timing mode for the production of rhythmic movements has been challenged. Indeed, tasks typically thought to exploit event-based timing have been shown to exhibit an emergent timing mode and vice versa (Huys et al., 2008; Studenka and Zelaznik, 2008; Zelaznik and Rosembaum, 2010; Studenka et al., 2012). These evidences suggested that processes for timing are more flexible than previously thought and that the event-emergent distinction is not an all-or-none difference (Repp and Steinman, 2010). As consequence, the relationship linking the two forms of temporal control is now a matter of debate.

Repp and Steinman (2010), using a condition in which tapping with left hand and circle drawing with right hand were performed simultaneously, showed that event-based and emergent timing can coexist when two different effectors perform different tasks, but also argued the possibility that the two timing modes could coexist in a single activity. On the other hand, Delignières and Torre (2011) rejected the possibility of a simultaneous expression of event-based and emergent timing in a single task. They showed, using an air tapping task, that the two forms of temporal processes represent two exclusive alternatives during the performance of a single task.

On the basis of the above-mentioned findings and theories we aim to address three questions in the domain of timing as result of sensori-motor integration. To accomplish these aims, we use in part the dataset already described in Bravi et al. (2014a) and obtained from a combined task of audio- and recall-motor integration in which sets of IWFEs are performed - while minimizing visual and tactile information - under different conditions (self-paced free from auditory constrain, driven by streams of paced clicks or by excerpts of paced music, and self-paced during recall of previous auditions) and at various tempi. Moreover, since in Bravi et al. (2014a, Table 1) a minimal part of the studied ranges of tempi was unequally distributed in terms of length, the original segmentation was slightly modified in order to achieve a continuous representation of the variable tempo.

In the wake of the discoveries about the ability of perceptual events to elicit event-based timing we first investigate whether simple and complex paced auditory stimuli, as streams of clicks and excerpts of music, influence differently the processes for temporal regulation of IWFEs. In particular, we want to study if music, although being not homogeneous and coming in many genres, has a different power to elicit the event-based timing with respect to the most commonly used streams of clicks. During the listening of music, the complexity inherent to beat perception (Patel and Iversen, 2014) could make the beat scarcely predictable and offer a poor temporal anchor for repetitive movements making them less discrete and, consequently, evoking emergent timing. Conversely, the listening to clicks could allow for an easy representation of the time intervals and produce an attraction toward the event-based management of timing (Zelaznik and Rosembaum, 2010). Therefore, we may hypothesize a priori that the ability of music to elicit the event-based timing should be somehow hampered by the intrinsic sound architecture; this hypothesis could be particularly plausible for high frequencies where the movement was shown to be less discontinuous (Huys et al., 2008; Repp, 2008b; 2011b).

Secondly, we explore whether the recall of an auditory stimulus, where auditory imagery is involved as an internal representation, is sufficient to influence timing control processes for the production of rhythmic movements. Our interest comes from the fact that in the millisecond timing research it was never taken into account whether the recall of audio information may be of significance for the difference between the two timing processes. However, little or nothing is known about the timing mechanisms active when the pacing stimulus is drawn using memory storages after short-term/working memory, i.e., those pertaining to intermediate-term and long-term memory (Kesner and Hopkins, 2006; Rosenzweig et al., 1993).

Finally, our IWFEs performed with no direct surface opposition and while minimizing visual information could potentially employ, as air finger tapping movements, both event-based and emergent timing processes (Spencer et al., 2003, 2007; Delignières and Torre, 2011). By using sets of IWFEs performed under different conditions and at various tempi, we want to get a better insight on whether the two timing modes are mutually exclusive or whether an event-based component can coexist with an emergent component. We chose to analyze our data by the windowed (lag one) autocorrelation $w\gamma(1)$, a recently introduced and reliable statistical method for the distinction between event-based and emergent timing (Lemoine and Delignières, 2009; Delignières and Torre, 2011), to reduce the positive bias on autocorrelation values provoked by the drift variance (Collier and Ogden, 2004) and to investigate the evolution of $\gamma(1)$ over time by identifying appropriately the underlying timing processes. The hybrid hypothesis proposed by Repp and Steinman (2010) would predict the possibility to observe near to zero series of $w\gamma(1)$ values over the entire duration of the set. Conversely, the mutually exclusive hypothesis by Delignières and Torre (2011) would predict the possibility to observe an alternation between epochs of positive and negative $w\gamma(1)$ values over time.

3.3 Methods

Participants for the present study are largely from the same cohort as those examined in a previous study (Bravi et al., 2014a). A new cohort composed of nine subjects was added in order to include the modifications of the original ranges of tempi. The set up, audio stimuli, data format, and structure of the session are fully described elsewhere (Bravi et al., 2014a) and are here summarized.

Participants

Eighty-seven right-handed volunteers took part in the study (forty males and forty-seven females, 18 to 27 years old). All were not musically trained and reported no auditory, motor, or other neurological impairments. Informed consent procedures were in accordance with local ethical guidelines (Comitato Etico Area Vasta Centro AOUCareggi, Florence, Italy) and conformed to the Declaration of Helsinki.

Set up

Each participant was tested individually, sitting upright on a chair with the feet on leg-rest, wearing eye-mask and headphones. The eye-mask prevented interference from visual information while headphones (K 240 Studio, AKG Acoustics GmbH, Wien, AT) were used to reduce environmental noise and to deliver audio information. The dominant forearm was placed in horizontal position supported by an armrest. The wrist and hand were free to move in mid-air. A triaxial accelerometer sensor (ADXL330, by Analog Devices Inc., Norwood, MA 02062), kept in position by an elastic band and secured by a Velcro strap, was positioned on the dorsal aspect of the hand, over the proximal part of the 2nd-3rd metacarpal bones. Sensor output was acquired and digitized at 200 Hz through PCI-6071E (12-Bit E Series Multifunction DAQ, National Instruments, Austin, TX, USA).

Audio stimuli

Stimuli were delivered binaurally to the participants through headphones. Audio stimuli (60s duration) were paced streams of clicks and excerpts of music. Clicks and music were selected to fit reference musical tempi chosen within the metronome markings from Adagio to Presto (Sachs, 1953), from 64 to 176 bpm (beats per minute – bpm – is the unit to measure tempo in music; our reference tempi are from 1.067 to 2.933 Hz, equivalent of 937.207 to 340.910 ms, Table 3). In Bravi et al. (2014a) the selected fourteen reference musical tempi were taken out of the original and generally accepted scale by Maelzel (Maelzel, 1818), with minor modifications. The same tempi were chosen for both streams of clicks and excerpts of music. To perform our analyses using tempo as a continuous variable, in the present study the tempi selection used in Experiment I (Bravi et al., 2014a) was slightly modified by the inclusion of the 160 bpm tempo, to replace the 162 bpm tempo, and of the 168 bpm tempo, for a total of fifteen reference tempi. Streams of clicks were produced using the audio editor Audacity (GNU/GPL, http://audacity.sourceforge.net/), via the function Generate Click (duration = 10ms, sound white noise). Music excerpts were extracted from original professional productions. The music fragments had a simple explicit rhythm and a stable tempo that remained constant throughout time. Since the determination of perceptual musical tempo can be ambiguous (McKinney and Moelants, 2007) and algorithms for tempo extraction have limitations (McKinney et al., 2007), three musical experts (professionals with musical experience) independently verified the tempo of the excerpts. Only fragments for which the experts collectively agreed of having a single musical tempo were selected. Music fragments were taken from a variety of musical genres popular among young people: rock, techno, dance, trance, hard rock, and film music. We used fragments from music productions, likely to be unfamiliar to the participants, since it was shown that familiarity with a song installs an accurate long-term memory of its tempo (Levitin and Cook, 1996; Quinn and Watt, 2006). Tempo variations of music fragments were analyzed, beat-mapped, and set to fixed bpm using the softwares Jackson (http://vanaeken.com/; accuracy is within a 0.001 bpm margin) and Audition (Adobe Systems Inc., San Jose, CA 95110-2704, USA). Time manipulations were all below 5% deviation of the mean music tempo (Dannenberg and Mohan, 2011), well under the threshold for detection of temporal changes in music (Ellis, 1991; Madison and Paulin, 2010). All audio files were normalized to -0.3 dB and stored as waveform (waveform audio file; 44.1 kHz; 16-bit depth; using Audition). Fade in and fade out (10 ms) were placed at the beginning and end of each file.

Data format

Sets of IWFEs were recorded during the session and kinematic parameters were evaluated. Data from the sensor were stored and an off-line analysis was implemented. Raw data from the triaxial accelerometer were elaborated to extract wrist's flexion-extension. The duration of a single wrist's flexion-extension was calculated as the difference between two consecutive wrist's flexions (see Bravi et al., 2014a) using a custom software developed in Matlab®. The tempi of the recorded IWFEs sets were ranked as ranges and IWFEs sets were assigned to a defined range according to their tempo (Table 3).

Session

The subject was instructed to restrain from listening to music during the day of the session. Each subject had participated in one single session. Overall, during a session, the performances of the IWFEs sets were originally executed under seven conditions (Bravi et al., 2014a). Since in this study we decided to focus our analyses on IWFEs sets performed in absence of auditory information (free, Fr), while listening to a stream of clicks or excerpt of music (Cl, Mu), and after 2 minutes from the end of the audio conditions (Cl2, Mu2, respectively), excluding the IWFEs sets performed after 5 min from the end of the audio condition (i.e., the conditions Cl5 and Mu5; Bravi et al., 2014a), the session is described accordingly (Fig. 4A, B). A single session was comprised of a baseline recording and 2 blocks. One block consisted of two pairs of Cl and Cl2 sets, or Mu and Mu2 sets, performed at two different reference tempi, for the auditory Cl or Mu sets; the same reference tempi were then used for the auditory sets of the second block. The order in which the clicks or music stimuli were presented was set to obtain equivalent number of subjects that received first one or the other.

Each session was preceded by a short practice test. After the practice test, the subject was asked if he/she felt comfortable with the task. Recordings from the practice test were not used for further analyses. No information was given to participants about the way to perform the tasks, in terms of discreteness or smoothness of movements (Delignières and Torre, 2011). The session started with recording in the Fr baseline condition, which consisted of three IWFEs sets. In the first set, the subject was asked to perform IWFEs in a self-paced manner. In the second set, the subject was asked to perform IWFEs faster than those of the first set. In the third set the subject was asked to perform IWFEs slower than those of the first recording. The three IWFEs sets in Fr condition were performed at the beginning of the session to avoid influences from previous synchronizations (as in the case of the recall conditions, see below).

The subject was then instructed to perform a set of repetitive IWFEs while listening to clicks or music at a similar pace concurrently with the tempo of the delivered audio (i.e., maintaining an in-phase 1:1 relationship between repeated wrist's flexion-extensions and the tempo of the audio, conditions Cl or Mu). Then, instructions to subject for IWFEs performances in recalls were of the kind: "now, try to hear in your head the auditory stimulus just listened to" (immediately after the end of the stimulus, see Zatorre and Halpern, 2005). After 2 minutes of mentally hearing the auditory stimulus, the subject was asked to perform IWFEs as accurately as possible at the tempo of the auditory stimulus while continuing to hear mentally the stimulus itself (conditions Cl2 or Mu2). The session continued with the recordings of IWFEs in a reversed order (i.e., with the Mu conditions if Cl was recorded first, or vice versa). In order to obtain a balanced number of performances for the chosen reference tempi, the two tempi that were selected for the blocks were randomized for each single session.

Also the session of the new cohort of subjects was comprised of a baseline recording and 2 blocks. The free baseline condition, differently from that in Bravi et al. (2014a), consisted of four IWFEs sets. In the first set, the subject was asked to perform IWFEs in a self-paced manner. In the second set, the subject was asked to perform IWFEs slower than those of the first set. In the third and fourth sets, the subject was asked to perform IWFEs faster than those of the first recording and then faster than those of the third recording (the free baseline condition in Fig. 4B). In addition, the two blocks consisted of two pairs of Cl and

Cl2 sets, or Mu and Mu2 sets, performed at two different reference tempi (160 bpm and 168 bpm) for the auditory Cl or Mu sets.

Since it was reported that time-series patterns can vary depending primarily on learning and several other brain factor (Pressing and Jolley-Rogers, 1997; Madison, 2004) and considering the fact that the goal of our experiment was not to analyze individual behavior, our session was deemed suitable for conducting this study seeing that each participant was asked to perform only a limited number of IWFEs sets at the same tempo. A similar strategy was already used to study synchronized human tapping (Kadota et al., 2004).

Finally, differences regarding the perception of music (Fujioka et al., 2004; 2005), the vividness of auditory images and the potency of their effects on skilled behavior observed between musicians and non-musicians (Aleman et al., 2000; Brodsky et al., 2003; Herholz et al., 2008); a possible different involvement of the two timing modes by musically trained than non-musicians when performing repetitive movements in different motor tasks (Baer et al., 2013); and the ability of the musicians to employ a different movement strategies to maintain accurate timing with respect to non-musicians (Baer et al., 2013) represented the reasons to study a homogenous group constituted by only musically untrained subjects.

Statistical methods

To investigate if, and to what extent, the processes for temporal regulation are influenced differently by the presence of auditory stimuli with different characteristics (Click versus Music) and to explore whether the recall of an auditory stimulus, where auditory imagination is involved, might influence timing control processes, we computed a series of (windowed) lag-one autocorrelations, herein abbreviated $w\gamma(1)$, for each set of IWFEs produced in the Fr, Cl, Mu, Cl2, and Mu2 conditions (Delignières and Torre, 2011). Lag-one autocorrelation is the autocorrelation of a series with itself, shifted by a particular lag of 1 observation. We computed w$\gamma(1)$ over a window of the 30 first points, moving the window by one point, all along the sets. Then, we calculated the mean of the obtained windowed lag series – mean w$\gamma(1)$ – for each set of IWFEs. We considered the mean w$\gamma(1)$ as an estimator of the overall autocorrelation in the set of IWFEs. Furthermore, we calculated percentage of positive w$\gamma(1)$ for each set of IWFEs. If not indicated otherwise, the mean w$\gamma(1)$ and the percentage of positive w$\gamma(1)$ of IWFEs are to be considered as the condition's and the range of tempi's means, respectively. Two separate two-way ANOVA analyses were conducted on mean w$\gamma(1)$ values and on percentages of positive w$\gamma(1)$ of the IWFEs sets to evaluate within-condition differences. The first factor considered in all ANOVA was the Condition (i.e., Fr, Cl, Mu, Cl2, and Mu2). The second factor was the Tempo, with fifteen ranges (as in Table 3). To take into account for multiple testing, ANOVA analyses were followed by Bonferroni post-hoc correction. We fixed the significance level at 0.05. In order to allow an appropriate use of parametric statistical tests, the Fisher's Z-transformation was used to normalize the distribution of autocorrelation coefficients (Nolte et al., 2004; Freyer et al., 2012).

Considering that w$\gamma(1)$ is computed over short windows, it results to be less affected than lag-one autocorrelation $\gamma(1)$ by the presence of long-range correlations that tend to induce positive bias (Delignières and Torre, 2011). Thus, the use of w$\gamma(1)$ appears more consistent with theoretically expected values (i.e., negative for event based timing, and positive for emergent timing) than $\gamma(1)$ calculated, instead, over the entire set. In addition, since w$\gamma(1)$ is aimed to detect a possible variation of the mean autocorrelation value over the duration of each set, it allows us to perform a more microscopic analysis that explores the evolution of lag-one autocorrelation over time. By this analysis we try to clarify about the dichotomy or continuum of timing modes controversy.

3.4 Results

The dataset

For the present study we analyzed 726 sets of IWFEs out of the original recordings. Criteria for the exclusion of the sets are described in Bravi et al. (2014a). IWFEs were performed under Fr, Cl, Mu, Cl2 and Mu2 conditions (n=153 for condition Fr, n=154 for Cl, n=134 for Cl2, n=147 for Mu, n=138 for Mu2) distributed over the 87 subjects, each containing a relatively high number of IWFEs (averaging from a minimum of 53.1, for condition Mu, range 1.017-1.133 Hz, to a maximum of 149.43, for condition Cl, range 2.883-3.000 Hz). For each set, we first calculated within-set mean and SD of IWFEs durations. Each within-set mean of the IWFEs durations was categorized within the appropriate rank (Table 3). ANOVA analyses on an equal number of sets per condition were performed (n=10 for rank 1, n=7 for rank 2, n=7 for rank 3, n=7 for rank 4, n=8 for rank 5, n=9 for rank 6, n=10 for rank 7, n=9 for rank 8, n=8 for rank 9, n=9 for rank 10, n=10 for rank 11, n=7 for rank 12, n=9 for rank 13, n=9 for rank 14, n=7 for rank 15).

Mean wγ(1) values and percentages of positive wγ(1) of IWFEs in the Fr and the audio conditions

We investigate if, and to what extent, the processes for temporal regulation are affected differently by the presence of simple and complex auditory stimuli. For comparisons we calculated mean wγ(1) values and percentages of positive wγ(1) of IWFEs (see: statistical methods section) under Fr, Cl and Mu conditions. The baseline was Fr condition.

Mean wγ(1) values and percentages of positive wγ(1) of IWFEs plotted per condition are shown in Figure 5. Mean wγ(1) was slightly positive for Fr condition, but negative for Cl, and slightly negative for Mu (Fig. 5A). Wγ(1) was more positive for Fr (61% of positive values) and widely more negative for Cl and Mu (only 30% and 37% of positive values, respectively; Fig. 5B).

Then, for Fr, Cl, and Mu conditions, we plotted mean wγ(1) values and percentages of positive wγ(1) of IWFEs as function of ranges of tempi. For the three considered conditions, mean wγ(1) appeared to change with movement durations (Fig 6A). In the Fr condition mean wγ(1) values were almost all positive. Overall, the Cl and Mu conditions showed negative mean wγ(1) values, but while in the Cl condition mean wγ(1) values resulted to be all negative, in the Mu condition were negative for only the first nine ranges of tempi. Mu condition expressed positive values from ranks 10 to 15 (Fig. 6C). Also percentages of positive wγ(1) of IWFEs appeared to be somewhat sensitive to movement durations (Fig. 6B). In the Fr condition percentages of positive wγ(1) were almost always above the 50%. In addition, while in the Cl condition percentages of positive wγ(1) resulted to be under the 50% for virtually all of ranges of tempi, the Mu condition expressed percentages of positive wγ(1) above the 50% at the high ranges of tempi, from ranks 10 to 15 (Fig. 6D).

To evaluate within-condition differences of mean wγ(1) values, the two-way ANOVA analysis was performed on Fr, Cl, and Mu, for Condition and Tempo factors. Results showed highly significant differences for the Condition (factor 1, $F_{2,333} = 74.421$, $p < 0.001$) and for the Tempo (factor 2, $F_{14,333} = 8.783$, $p < 0.001$). The interaction between the Condition and the Tempo showed a highly significant p-value ($F_{28,333} = 1.931$, $p < 0.01$). Bonferroni post-hoc tests among groups of factor 1 (Condition) showed highly significant differences between different conditions, substantiating that mean wγ(1) values of self-paced IWFEs, free from auditory constrain, were different from those of IWFEs performed in synchrony with paced auditory inputs but also that click and music affected differently the mean wγ(1) of IWFEs.

To evaluate within-condition differences of percentages of positive wγ(1), the two-way ANOVA was performed on Fr, Cl, and Mu. Results showed highly significant differences for the Condition (factor 1, $F_{2,333} = 55.430$, $p < 0.001$) and for the Tempo (factor 2, $F_{14,333} = 6.899$, $p < 0.001$). The interaction between the Condition and the Tempo showed a significant p-value ($F_{28,333} = 1.591$, $p < 0.05$). Bonferroni post-hoc tests in general confirmed results obtained for the mean wγ(1) values, apart from difference between Cl and Mu ($p > 0.05$).

It was apparent, however, that at the high tempi (ranks 10 to 15) mean wγ(1) values and percentages of positive wγ(1) in the Mu condition diverged evidently, moving towards positive values, from the negative mean wγ(1) values and percentages of positive wγ(1) of the Cl condition (Fig. 6C, D). This was extended by two-way ANOVA analyses on mean wγ(1) values and percentages of positive wγ(1) performed separately for the first nine ranges of tempi (ranks 1 to 9) and for the last six ranges of tempi (ranks 10 to 15).

For the first nine ranges of tempi results demonstrated highly significant differences for the Condition (factor 1, $F_{2,198} = 61.157$, $p < 0.001$, for mean wγ(1) values; $F_{2,198} = 50.490$, $p < 0.001$, for percentages of positive wγ(1)) and for the Tempo (factor 2, $F_{8,198} = 4.255$, $p < 0.001$, for mean wγ(1) values; $F_{8,198} = 3.453$, $p < 0.001$, for percentages of positive wγ(1)). The interactions between the Condition and the Tempo showed no significant p-values ($F_{16,198} = 1.052$, $p > 0.05$, for mean wγ(1) values; $F_{16,198} = 0.479$, $p > 0.05$, for percentages of positive wγ(1)). Both in the case of mean wγ(1) values and percentages of positive wγ(1) Bonferroni post-hoc tests among groups of factor 1 provided highly significant differences between Fr and Cl ($p < 0.001$) or Fr and Mu ($p < 0.001$) but no significant differences between Cl and Mu ($p > 0.05$).

On the contrary, for the last six ranges of tempi the two-way ANOVA analyses demonstrated highly significant differences for the Condition (factor 1, $F_{2,135} = 22.279$, $p < 0.001$, for mean wγ(1) values; $F_{2,135} = 14.861$, $p < 0.001$, for percentages of positive wγ(1)) but no significant differences for the Tempo (factor 2, $F_{5,135} = 0.088$, $p > 0.05$, for mean wγ(1) values; $F_{5,135} = 0.102$, $p > 0.05$, for percentages of positive wγ(1)). The interactions between the Condition and the Tempo showed no significant p-values ($F_{10,135} = 1.307$, $p > 0.05$, for mean wγ(1) values; $F_{10,135} = 1.132$, $p > 0.05$, for percentages of positive wγ(1)). Bonferroni post-hoc tests continued to provide highly significant differences between Fr and Cl ($p < 0.001$). Moreover, it is important to note that no significant differences between Fr and Mu ($p > 0.05$) were found while highly significant differences were obtained between Cl and Mu ($p < 0.001$).

This latter result together provided evidence that streams of clicks and excerpts of music influence differently mean wγ(1) values and percentages of positive wγ(1) specifically for the fast rhythmic movements.

Mean wγ(1) values and percentages of positive wγ(1) in Fr and Recall conditions

We here investigate if the evocation of auditory imagery during the rhythmic motor performance might influence timing control processes. For comparisons we calculated mean wγ(1) values and percentages of positive wγ(1) of IWFEs under the Fr, Cl2, and Mu2 conditions. In imagery research the comparison of tasks in which participants are instructed to generate auditory imagery (Cl2 and Mu2) to tasks in which participants are not instructed to generate auditory imagery (Fr) is one type of data to be survey (Hubbard, 2010).

Mean wγ(1) values and percentages of positive wγ(1) of IWFEs were plotted per condition (Fig. 7A, B). Mean wγ(1) was somewhat negative for Cl2 and for Mu2, compared to the slightly positive value for Fr condition (Fig. 7A). Moreover, wγ(1) values were also somewhat more negative for Cl2 and Mu2 (45% and 45% of positive values, respectively) and, when compared to the more positive wγ(1) values of Fr (61% of positive values), presented a particularly intermediary profile with a more balanced distribution between negative and positive wγ(1) (Fig. 7B).

When the Fr, Cl2, and Mu2 mean wγ(1) were plotted as function of ranges of tempi (Fig. 8A, C), mean wγ(1) values appeared to change, to some extent, with movement durations. In the Cl2 and Mu2 conditions mean wγ(1) values were mostly negative (eleven on fifteen in Cl2 and ten on fifteen in Mu2, respectively). In the Fr condition mean wγ(1) values were almost all positive. Also when the Fr, Cl2, and Mu2 percentages of positive wγ(1) of IWFEs were plotted as function of ranges of tempi (Fig. 8B, D), percentages of positive wγ(1) appeared to change, to some extent, with movement durations. In the Cl2 and Mu2, but not in Fr, percentages of positive wγ(1) were, though in most of cases very closed to 50%, often under the 50%.

To evaluate within-condition differences of mean wγ(1) values and of percentages of positive wγ(1), two-way ANOVA analyses were performed, on Fr, Cl2, and Mu2, for the Condition and the Tempo factors. Results demonstrated highly significant differences for the condition (factor 1, $F_{2,333}$ = 22.751, $p < 0.001$, for mean wγ(1) values; $F_{2,333}$ = 16.957, $p < 0.001$, for percentages of positive wγ(1)) and significant differences for the tempo (factor 2, $F_{14,333}$ = 2.030, $p < 0.05$, for mean wγ(1) values; $F_{14,333}$ = 1.919, $p < 0.05$, for percentages of positive wγ(1)). The interactions between the Condition and the Tempo showed no significant p values ($F_{28,333}$ = 0.641, $p > 0.05$, for mean wγ(1) values; $F_{28,333}$ = 0.462, $p > 0.05$, for percentage of positive wγ(1)). Both in the case of mean wγ(1) values and percentages of positive wγ(1) post-hoc tests among groups of factor 1 showed highly significant differences between baseline Fr and Cl2 ($p < 0.001$) or Fr and Mu2 ($p < 0.001$) but no significant differences between Cl2 and Mu2 ($p > 0.05$), revealing that auditory experience, constructed of components drawn from memory in absence of direct sensory instigation of experience, influences both mean wγ(1) values and percentages of positive wγ(1).

3.5 Discussion

Our data show that mean wγ(1) and percentages of wγ(1) of IWFEs durations, in the audio synchronization Cl and Mu conditions, are biased toward negative values (the domain of the event-based timing) as compared with the baseline Fr condition. This latter is mostly characterized by positive values (the domain of the emergent timing), and the difference between the audio conditions and the baseline is highly significant. Delignières and Torre (2011) argued that event-based timing is not determined by «the presence of motor events, or any external events such as metronomic signals, but by the presence of cognitive events provided by an internal timekeeper that trigger motor responses» (Delignières and Torre, 2011, p. 317) and disagree with the idea that synchronization should necessarily imply event-based timing. We show that paced auditory information may favor, together with a rhythmic movement task, an abstract representation of the time intervals to produce.

In addition, the movement duration has an evident influence on mean wγ(1) values and percentages of positive wγ(1) of IWFEs. What appears from our data is that as movement durations decrease the emergent component of timing for IWFEs is favored, independently from the condition. Discrete slow and continuous fast tapping are considered to be two distinct topological classes, with the first requiring a clock-like process and the second a self organized oscillatory process (Huys et al., 2008). As the frequency of a discontinuous movement increases, the movement resembles an oscillation and the processing can be equated with emergent timing (Repp, 2008b; 2011b). In agreement with the latter interpretation, we found the highest mean wγ(1) values and percentages of positive wγ(1) mostly for fast IWFEs.

More in detail, our findings provide evidence that, specifically for the fast movements, clicks and music favor differently the elicitation of the event-based timing. During the performance of fast movements music, unlike clicks, seems to lack the power of counteracting the shift of $w\gamma(1)$ toward positive values as frequency of movements increase. In other words, at the fastest tempi music is too amorphous to evoke the event-based timing that the difference between the baseline Fr and the Mu conditions, conspicuous for the adagio to moderato tempi, vanishes for the allegro to presto tempi.

The synchronization of responses to metronome and the self-paced condition differ since the former is characterized by the contribution of error correction processes, working to prevent large asynchronies and tempo drift (Semjen et al., 2000; Repp, 2005). The type of movement and the corresponding pacing characteristics used to specify the timing target additionally influence the accuracy of sensorimotor synchronization processes (Lorås et al., 2012).

It was shown that the adjustment of movement trajectories is correlated to degree of correction of synchronization errors and, consequently, to the accuracy of synchronization with paced clicks. Balasubramaniam and colleagues (2004) have shown that synchronization with clicks increases the asymmetry of movement trajectories and that, if the goal is to maximize the engagement with an external auditory input, the better strategy is to move discretely because discrete movements support a faster phase correction (Balasubramaniam et al., 2004). Since no information was given to our participants in terms of discreteness or smoothness of the movements to be performed, it is possible to hypothesize that clicks, characterized by punctuate perceptive markers provide an efficient temporal anchor (Zelaznik and Rosembaum, 2010) affecting IWFEs during synchronization even at high frequencies by nudging movement from continuous to discrete. Discrete movements offer more salient sensory information on which phase correction is based (Elliott et al., 2009).

Both discrete movements and a faster phase correction could lead to an augmentation of the event-based component for the production of IWFEs. It was shown that production of discrete movements demands a neural structure, or a network of structures, not implicated in the implementation of the dynamics for motion (Huys et al., 2008). Moreover, fast phase correction during synchronization is assumed to increase the event-based component for the production of rhythmic movements. Indeed, as is predicted by extensions of the two-level model to synchronization, slow correction tends to introduce positive correlations between successive movements, whereas fast correction tends to introduce alternations between shorter and longer movements and thus negative correlation (Semjen et al., 2000; Vorberg and Schulze, 2002; Repp and Steinman, 2010).

Identification of musical beat involves perception of a periodic series of regularly recurring, quite equivalent, mental events that have to be extrapolated from spectro-temporally complex sound sequences (Large and Snyder, 2009; Patel and Iversen 2014). Musical beats can be perceived across a wide range of tempi (Van Noorden and Moelants, 1999) and influence how subjects organize the elements of the rhythm both as figural and metric codes (London, 2012). Intervals between 1200 and 400 ms bring about the strongest sense of beat, with a preference for periods around 600 ms (London, 2012). Moreover, in a walking synchronization task participants did not synchronize with the music especially at the highest tempi (between 146 and 190 bpm, i.e., between 2.433 and 3.167 Hz; Styns et al., 2007). Also, cutaneous mechanoreceptive afferents participate in the perception of musical meter, and information from audition and touch is grouped into a common percept (Huang et al., 2012). Thus, the complexity inherent to the perception of musical beat, along with the performance of movements lacking additional tactile information, could make the beat scarcely predictable for fast movements and offers a poor temporal anchor for the transformation of oscillatory IWFEs to discrete, a motor conversion strategy engaged during fast phase correction in a synchronization condition (Elliott et al., 2009). All of which makes music inadequate to elicit the event-based timing process for the production of IWFEs at high frequencies.

Additional basis for the distinction between event-based and emergent timing resides in the auditory representation of movement (Zelaznik and Rosenbaum, 2010). Also, auditory imagery refers to the aspect of cognition in which auditory information is internally generated and processed in the absence of real sound perception (Herholz et al., 2012). With these premises, we investigated whether auditory imagery might influence timing control processes for motor production. We show that in recall conditions, timing for movements shift toward a more event-based scenario as compared to the Fr condition where the emergent component predominates.

The production of rhythmic movements had been widely-employed for the study of timing. The most common paradigm used to explore timing is the synchronization-continuation task, introduced by Stevens in 1886 (Lorås et al., 2012). In this paradigm, subsequent to the stop of the sensory stimulus subjects attempt to represent the interval duration of stimulus with a sustained and periodic motor act by retrieval of the pre-learned durations (continuation phase; Coull et al., 2011). A large amount of knowledge of the mechanisms for timing is derived from analyses performed on the continuation phase in which auditory imagery was shown to be exploited during performance (Rao et al., 1997). Our result indicates that even the simple recall of an auditory stimulus appears to be sufficient in influencing timing mechanisms.

Also, it is also interesting to note that the recall of music is more efficient than music in invoking the event-based component at the high tempi (compare Fig. 6A-D with Fig. 8A-D). The ability to build a mental representation of an auditory input is always possible, but varies among people (White et al., 1977) and is influenced by training, or by musical experiences in perception and performance (Keller and Koch, 2008; Hubbard, 2010). Halpern (1992) showed that, when participants imagine familiar music and tap a finger along with the imaged beat, musical experience increases the spreading of tempo representation within auditory imagery. In our task in which the goal is to perform as precisely as possible sets of isochronous movements, the augmented difficulty to represent the music tempo in non-musicians could bias subjects toward the musical beat by reducing the weight of other characteristic (musical contour, melody, and harmony). This transformed representation could paradoxically make the imagined beat decisive to shape more discrete IWFEs and to invoke the event-based component of timing.

Event-based and emergent timing have been investigated for years using prototypical tasks. Using finger tapping, for the event-based timing, and circle drawing or forearm oscillation, for the emergent timing, the two forms of timing were regarded as mutually exclusive (Robertson et al., 1999; Zelaznik et al., 2002; Delignières et al., 2004). This mutual exclusiveness was first challenged by Repp and Steinman (2010). Using our IWFEs, performed under different conditions and at various tempi, we tried to clarify the exclusiveness versus coexistence of timing processes and their possible interrelationship. We predicted a close-to-zero $w\gamma(1)$ series over duration of entire set in case of the hybrid model (Repp and Steinman, 2010), or to observe an alternation between positive and negative $w\gamma(1)$ values over the duration of the entire set in case of mutually exclusive model (Delignières and Torre, 2011).

We discuss our observations by showing the entire data board used for performing ANOVA analyses – per condition and ranges of tempi – as timed series of $w\gamma(1)$ for each set of IWFEs (Figs. 9-11). Our data board shows unequivocally that participants, in favor of the mutual exclusive model and in contrast with the hybrid model, can exploit either the event-based or the emergent timing mode, or the two mode in alternation, but in all cases each mode appears to be exclusive (see series color coded in Figs. 6-8). It is evident, once again, that the emergent component of timing becomes stronger and prevails on event-based component as the tempo of movements increases, in spite of the alternation of timing modes and in good agreement with Repp (2008b). Also, while the alternation of timing modes has been described in the continuation phase of a rhythmic motor task (Delignières and Torre, 2011), we find that it is also present in conditions in which participants had to synchronize to an audio stimulus, indicating that timing modes alternation is not evident only in absence of auditory input.

A final metaphor to bring together our data may come from the synchronization of musicians in an ensemble during performance. The conductor uses baton movements to give cues for expressive character, including dynamics and *accelerando* or *ritardando* in timing. Although conventions are recognized for conducting in different tempi, there are no standards for defining the beat. Thus, the point on the movement that is considered to mark the beat may vary among conductors. Conductors' movement trajectories can frequently appear smooth and continuous. However, skilled musicians develop great sensitivity to baton movements, and studies have shown that points of relatively high acceleration are picked out by the players to define events for synchronization (Luck and Toiviainen, 2006; Luck and Sloboda, 2008). We can infer that also our subject has no standards for defining the timing mode. Thus, timing mode may vary, depending from the motor task and the sensory input, and the subject alternates from one to the other seemingly to optimize performance, as event-based and emergent timing complement each other (Semjen, 1996). However, subjects develop a great sensitivity to be in time (Janata et al., 2012) and tend to favor epochs of emergent timing as movements become fast enough to be difficult to manage with event-based timing. Further studies are needed to explore this latter hypothesis and, as also recently claimed in an elegant study of auditory-motor coupling on human gait (Hunt et al., 2014), to initiate capitalization on the potential that auditory-motor coupling offers especially in the field of neuromuscular rehabilitation.

Chapter 4: Experiment III

A little elastic for a better performance: kinesio taping of the motor effector modulates neural mechanisms for rhythmic movements

4.1 Abstract

A rhythmic motor performance is brought about by an integration of timing information with movements. Investigations on the millisecond time scale distinguish two forms of time control, event-based timing and emergent timing. While event-based timing asserts the existence of a central internal timekeeper for the control of repetitive movements, the emergent timing perspective claims that timing emerges from dynamic control of nontemporal movements parameters. We have recently demonstrated that the precision of an isochronous performance, defined as performance of repeated movements having a uniform duration, was insensible to auditory stimuli of various characteristics (Experiment I, Bravi et al., 2014a). Such finding has led us to investigate whether the application of an elastic therapeutic tape (Kinesio® Tex taping; KT) used for treating athletic injuries and a variety of physical disorders, is able to reduce the timing variability of repetitive rhythmic movement. Young healthy subjects, tested with and without KT, have participated in sessions in which sets of repeated IWFEs were performed under various auditory conditions and during their recall. Kinematics was recorded and temporal parameters were extracted and analyzed. Our results show that the application of KT decreases the variability of rhythmic movements by a twofold effect: on the one hand KT provides extra proprioceptive information activating cutaneous mechanoreceptors, on the other KT biases toward the emergent timing thus modulating the processes for rhythmic movements. Therefore, KT appears able to render movements less audio dependent by relieving, at least partially, the central structures from time control and making available more resources for an augmented performance.

4.2 Introduction

Considerable evidence suggest that the study of human motor rhythmic performance synchronized to auditory stimuli is useful in unraveling neural aspects of action timing. The effects of different types of audio information (i.e., metronome or music) on motor performance have been extensively investigated in studies of finger tapping (Repp, 1999a; 1999b; del Olmo and Cudeiro, 2005) and of gait (see: Wittwer et al., 2013). The interest for the effects of paced auditory stimuli on rhythmic activities stems from the proven notion that this design of sensorimotor integration is shown to be an effective tool for gross motor rehabilitation in neurological diseases by improving spatial-temporal parameters and decreasing temporal variability (Thaut et al., 1996; McIntosh et al., 1997; del Olmo and Cudeiro, 2005; del Olmo et al., 2006; Hausdorff et al., 2007; Arias and Cudeiro, 2008; de Dreu et al., 2012).

In a recent study we showed how do auditory stimuli with distinct characteristics, streams of clicks or excerpts of music, influence the precision of repeated IWFEs, performed with no direct surface opposition and minimizing visual information (Bravi et al., 2014a). Some reports have described a reduction of temporal variability for rhythmic movements in the presence of paced auditory stimuli. Our data, however, displayed clearly that when both tactile and visual information are minimized, the listening alone to paced auditory stimuli does not improve the precision of an isochronous performance. Also, in a previous study on timing of rhythmic movements a lack of reduction in temporal variability was observed during paced tapping when compared to unpaced tapping (Schlerf et al., 2007). These findings have prompted us to investigate other tools that might augment the precision of rhythmic movement.

In addition, investigations on the millisecond time scale distinguish two forms of time control, explicit timing and implicit timing, later renamed as event-based timing and emergent timing, respectively (Spencer and Ivry, 2005). Event-based timing has evolved from the information processing approach, asserting the existence of internal timekeepers for motor control, and is well represented by the two-level model proposed by Wing and Kristofferson (1973a, b). According to the Wing and Kristofferson model, temporal precision in a self-paced tapping is limited by variability in the central timekeeper and by variability arising from the peripheral motor system (Semjen et al., 2000). The emergent timing perspective is derived from the dynamic systems theory, claiming that there are no representational clocks (Kelso, 1995; Kugler et al., 1980) and that timing emerges from dynamic control of nontemporal movements parameters (Huys et al., 2008; Schoner, 2002) such as stiffness which is playing a major role for determining movement frequency (Turvey, 1977; Delignières et al., 2004). For the study of timing, the task most widely employed was the performance of repeated movements. Among the rhythmic motor tasks, tapping is thought to be under the control of the event-based timing while circle drawing is thought to be under the control of the emergent timing (Zelaznik et al., 2002). Air tapping, a motor task performed in the air with no surface contact, represents a more recent approach for the study of timing. This motor task possesses specific characteristics of both the event-based and emergently motor rhythmic tasks due to the presence of salient motor events and smooth effector trajectories (Delignières and Torre, 2011).

The participation of the cerebellum in timing was once a controversial issue (Leiner et al., 1993; Rao et al., 2001). To date, the cerebellar timing hypothesis, first formulated by Keele and Ivry (1990), is widely accepted. According to this hypothesis, the cerebellum functions as an internal timing device in the milliseconds range for both motor and non-motor processes (Ivry and Spencer, 2004). In particular, the involvement of the inferior olive and the climbing fiber system in timing was shown to take part in encoding temporal information independent of motor behavior (Xu et al., 2006). Investigations using rhythmic tapping tasks have provided evidences to support this hypothesis. In a study on individuals with unilateral cerebellar lesions, participants were asked to perform timed tapping, intermittent circle drawing, and continuous circle drawing tasks. Performances were impaired only when tasks were executed with the ipsilesional hand and involved movements theorized to require event-based but not emergent timing (Spencer et al., 2003).

The timing mode of rhythmic movements can change over time within a single task (Studenka and Zelaznik, 2008; Zelaznik and Rosenbaum, 2010; Delignières and Torre, 2011). The discrete or continuous character of movements performed in the rhythmic tasks is considered to be a key factor for the involvement of the event-based or the emergent timing mode (Robertson et al., 1999; Huys et al., 2008). In addition, neurophysiological and neuroanatomical studies provided bases to suggest that neural circuits are not completely independent of the timing functions. For discrete movements, it is proposed that explicit processes for timing arise as coordinated activity in the core striatal and olivo-cerebellar networks that are interconnected, with each other and with the cerebral cortex, through multiple synaptic pathways (Spencer et al., 2007; Teki et al., 2012). Conversely continuous movements, by nature, lack an event structure. For these movements timing may be achieved through the control of a secondary variable, such as angular velocity, which does not involve the cerebellum.

Kinesio® Tex Tape is an elastic cotton strip with an acrylic adhesive developed by Japanese chiropractor, Dr. Kenso Kase, in the 1970's (Kase et al., 2013). Kinesio® Tex taping (KT) is a kinesthetic method commonly used in clinical practice for treating athletic injuries and a variety of physical disorders, with the purpose of mimicking the thickness and flexibility of the skin (Morris et al., 2013). It is claimed that the application of KT causes micro convolutions, or folds, in the skin; it brings about a lifting of the skin away from the tissue beneath, favoring the release of pressure from tender tissues underneath and providing space for lymphatic fluid movement (Morris et al., 2013).

It was proposed that KT is able to enhance somatosensory inputs and influence proprioception through stimulation of cutaneous mechanoreceptors (Callaghan et al., 2002; Halseth, 2004; Kneeshaw, 2002). We have, therefore, chosen KT as a tool for possibly augmenting the precision of rhythmic movements. While little is known about the potential proprioceptive effect of KT, the stimulation of cutaneous mechanoreceptors is believed to be induced by the pressure and stretching effect provoked by KT application on the skin (Grigg, 1994).

In the current study we investigate whether the application of KT on skin is able to reduce the timing variability of repetitive rhythmic movements. We also attempt to understand whether a causal relationship subsists between such reduction and functional augmentation of central structures involved, brought about by relieving, at least partially, these structures from time control.

We thus performed an experiment in which subjects, tested with and without KT, participated in sessions in which sets of repeated IWFEs were performed under different conditions (i.e., without audio information, with paced audio in the form of clicks or music, and in the recall conditions; see above Experiments I and II). Our IWFEs performed with no direct surface opposition and while minimizing visual information, could potentially employ, as air finger tapping movements, both event-based and emergent timing processes. Participants were not instructed about the way to perform the IWFEs since it was showed that in the absence of specific instructions, the production of movements with no contact surface elicits alternatively different timing modes (Delignières and Torre, 2011).

We hypothesize that KT, due to its aforementioned characteristics, is able to cause an improvement of the wrist joint proprioception due to augmented afferent input via the stimulation of cutaneous mechanoreceptors (Riemann and Lephart, 2002). The improvement in wrist joint proprioception would stabilize the motor effector during the performance, causing the IWFEs to be less discrete and thus smoother. Consequently this would entail the shifting from an event-based to emergent process to control the production of the IWFEs (Spencer et al., 2007; Huys et al., 2008). Therefore, by relieving, at least partially, the central structures from timing control, KT would release resources and allow for a net augmentation of the central efficiency and, consequently, reduce the timing variability of IWFEs.

4.3 Methods

Participants

A group of 25 right-handed volunteers (21 males, ages 20-27, mean 24.1±2.4 years; 4 females, ages 18-27, mean 23.0±2.7 years) took part in the recording sessions. All participants were naive to the purpose of the study; they were neither musically trained nor listeners of a classical music repertoire, and reported no auditory, motor, or other neurological impairments. The experimental protocol conformed to the requirements of the Federal Policy for the Protection of Human Subjects (U.S. Office of Science and Technology Policy) and of the Declaration of Helsinki, and has been approved by the Research Ethics Board of our Institution (Comitato Etico Area Vasta Centro AOUCareggi, Florence, Italy). All participants provided an informed consent in written form.

Set up

Each subject was tested individually, sitting upright on a chair with the legs comfortably positioned on leg-rest (Fig. 12A). The participant's right forearm was placed on the armrest, in a relaxed horizontal position. The wrist and hand of the subject were free to move in mid-air with no direct opposition, thus minimizing tactile information. In order to reduce possible interference of visual information, the subject was requested to wear a blindfold. Environmental noise was reduced by the use of headphones (K 240 Studio, AKG Acoustics GmbH, Wien, AT), which were also used for the clean delivery of audio information. This setup was designed to minimize all information that is known to influence motor strategies (i.e., visual, tactile, and environmental noise) and that may result in a different motor performance (Bove et al., 2009; Saijo and Gomi, 2010). A triaxial accelerometer (ADXL330, Analog Devices Inc., Norwood, MA 02062) was placed on the dorsal aspect of the hand, over the proximal part of the 2nd-3rd metacarpal bones. The sensor, placed in a small pocket, was kept in position by an elastic band and secured by a Velcro strap. Sensor output was acquired and digitized at 200 Hz through PCI-6071E (12-Bit E Series Multifunction DAQ, National Instruments, Austin, TX, USA).

Audio Stimuli

Audio stimuli were paced streams of clicks and excerpts of music. Music excerpts of 60 sec duration were extracted from original professional productions. Selected fragments had a simple and explicit rhythmic structure and a tempo that remained constant throughout time. Music fragments were taken from musical styles popular among young people: rock, techno, dance, trance, hard rock, and film music. Three musical experts (professionals with musical experience) were asked to verify independently the tempo of the excerpts in order to be as accurate and sure as possible in the choice of unambiguous paced excerpts. It is known that the determination of perceptual musical tempo can be ambiguous (McKinney and Moelants, 2007) and that algorithms for music tempo extraction have several limitations (McKinney et al., 2007), although recent effort has been put into methods to possibly improve the evaluation metrics used for automatic tempo estimation (Levy, 2011). Only fragments for which the experts collectively agreed of having a single musical tempo were selected. All chosen fragments had small tempo variations due to live performance. Therefore, the tempo for each fragment was analyzed, beat-mapped, and set to fixed beats per minute (bpm, used as a measure of tempo in music) using the softwares Jackson (http://vanaeken.com/; accuracy is within a 0.001 bpm margin) and

Audacity (GNU/GPL, http://audacity.sourceforge.net/). Our time manipulations were all well below 5% deviation of the mean music tempo (professional performances have minimal deviations from mean tempo; Dannenberg and Mohan, 2011) and thus below the detection threshold for temporal changes in music (Ellis, 1991; Madison and Paulin, 2010). We didn't use fragments likely to be familiar to the listeners since it has been shown that high familiarity with a song installs an accurate long-term memory of its tempo (Levitin and Cook, 1996; Quinn and Watt, 2006). Streams of clicks of 60 sec duration were produced using the audio editor Audacity, via the Generate Click Track function. The duration of an individual click was set to 10 ms and the click sound was set to white noise. The music and clicks stimuli were set to eight reference tempi ranging from 64 to 176 bpm (937.21 to 340.95 ms, Table 4). The same eight tempi were chosen for both streams of clicks and excerpts of music. Audio files were all normalized to -0.3 dB as the highest peak and stored as waveform (waveform audio file; 44.1 kHz; 16-bit depth) using Audacity. Fade in and fade out (10 ms) were placed at the beginning and end of each file. Audio stimuli were presented binaurally to the subjects through headphones (Fig. 12A).

Data format

Subjects were asked to perform sets of IWFEs and kinematic parameters were evaluated. Data from the sensor were stored and an off-line analysis of raw data from the triaxial accelerometer was implemented. The signal extracted from the accelerometer presented a minimum when the wrist reached the maximum flexion and a maximum when it reached the maximum extension. The duration of a single wrist's flexion-extension (i.e., IWFE duration) was calculated as the difference between two consecutive flexion-extension minima (custom software developed in Matlab®). To avoid initial and final transients, the first and last 5 seconds of each recording were excluded from analysis (Repp, 2005; 2011a). Considering that tempi of the recorded IWFEs sets were remarkably variable, giving rise to a quantitative redundancy of tempi obtained in overall, we have decided to rank them as ranges (Table 4). IWFEs sets were then assigned to a defined range according to their tempo.

Sessions

Each subject had participated in two sessions, one with no KT (N-KT) and one with KT (Fig 12B), that were performed at a week's distance. The order in which subjects performed the N-KT or KT sessions were set to obtain equivalent number of subjects that played first one or the other. The KT session started approximately 10 minutes after mounting the tape since this interval is needed to overcome perception of tape on the skin (Kase et al., 2013). In each session the subject performed 16 sets of repeated IWFEs under various conditions. A single session was comprised of a baseline recording (4 sets) and 2 blocks (12 sets). In a single session the performance of the IWFEs sets was executed under five conditions: in absence of auditory information (free, Fr), while listening to a stream of clicks (Cl), after 2 minutes from the end of the Cl condition (Cl2), while listening to an excerpt of music (Mu), after 2 minutes from the end of the Mu condition (Mu2). Sets of IWFEs were recorded in all conditions. For each block IWFEs sets were performed using one type of auditory stimulus (Cl or Mu). One block consisted of three pairs of Cl and Cl2 sets, or Mu and Mu2 sets, performed at three different reference tempi, for the auditory Cl or Mu sets; the same tempi were then used for the auditory sets of the second block (Fig. 12B). The order in which the clicks or music stimuli were presented was set to obtain equivalent number of subjects that received first one or the other.

The subject was instructed to restrain from listening to music during the day of the session. Each session began with instructions on how the sets of wrist's flexion-extensions were to be performed, followed by a short practice test. During the practice test, IWFEs were recorded and evaluated to assess whether the instructions were understood; after the practice test, the subject was asked if he/she felt comfortable with the task. Recordings from the practice test were not used for further analyses. The session started with recording in the Fr condition, which consisted of four IWFEs sets. In the first set, the subject was asked to perform IWFEs in a self-paced manner. In the second set, the subject was asked to perform IWFEs slower than those of the first set. In the third and fourth sets, the subject was asked to perform IWFEs faster than first recording and then faster than the third recording. The subject was then instructed to perform a set of repetitive IWFEs while listening to clicks or music at a similar pace concurrently with the tempo of the delivered audio (i.e., maintaining an in-phase 1:1 relationship between repeated wrist's flexion-extensions and the tempo of the audio, conditions Cl or Mu). Then, instructions to subject for IWFEs performances in recalls were of the kind: "now, try to hear in your head the auditory stimulus just heard" (immediately after the end of the stimulus, see Zatorre and Halpern, 2005). After a 2min break, the subject was asked to perform IWFEs as accurately as possible at the tempo of the auditory stimulus just heard while concurrently hearing mentally the stimulus itself (conditions Cl2 or Mu2). The session continued with the recordings of IWFEs in a reversed order (i.e., with the Mu conditions if Cl was recorded first, or vice versa). In order to obtain a balanced number of performances for the eight chosen reference tempi, the three tempi that were selected for the blocks were randomized for each single session.

Kinesio® Tex Tape application

The Kinesio® Tex Tape is comprised of a polymer elastic strand wrapped by 100% cotton fibers. It allow for a longitudinal stretch of 55-60% of its resting length. The Kinesio® Tex Tape is applied to the paper substrate with 25% of tension; the adhesive is 100% acrylic (Kase et al., 2013). For the KT (Kinesio® Tex Gold™ FP - 2" Red) application the subject, already seated on the chair with own right forearm rested on the armrest, was asked to keep the wrist in a position of maximum flexion, and the distance between the lateral epicondyle of the humerus and the distal end of the third phalanx of the middle finger was measured. The purpose was to apply the tape over the open kinetic chain including wrist, metacarpal, and finger joints. During the application of KT, between the lateral epicondyle of the humerus and phalanges, the wrist and forearm were maintained in full flexion and full pronation, respectively (Fig.12C). After manually assessing the origin and insertion of muscles, KT was applied over the extensor carpi ulnaris, extensor carpi radialis longus and brevis, extensor digitorum, extensor indicis, extensor digiti minimi, and extensor pollicis longus (Fig 12D-F). The strip of Kinesio® Tex was cut 5 cm longer than the maximum length of the kinetic chain measured with the wrist in maximum flexion (Kase et al., 2013). The course of the tendons of the extensor muscles (for each finger) was then identified on the back of subject's hand and distances were measured between the distal end of each phalanx and the wrist. Measurements were used to cut the distal side of the elastic band into five branches to be placed over the metacarpal area and fingers following the course of the tendons. KT was then applied from 5 cm proximal to muscles insertion to facilitate muscle function; the application tension was light, about 25%. From the lateral humeral epicondyle, KT was applied - in a wave-like pattern - to wrap the wrist's extensors until reaching the wrist. Each branch was then applied down on the back of phalanx until the nail.

Statistical analysis

To model directly the observed IWFEs durations we adopted random effect ANOVA models for repeated measurements (Diggle et al., 2002; Pinheiro and Bates, 2000). Separate models were adopted for different kinds of conditions and also the response variable was chosen differently according to the presence of audio. In particular, the differences between observed and the expected IWFEs durations were considered as response variable for performances under audio (Cl and Mu) and recall (Cl2 and Mu2) conditions. This response variable measures the error observed in the IWFEs durations, the observed IWFEs duration was instead considered as the response variable for performances in the Fr condition.

As the response variables have been recorded several times for each performance and for each individual, a random effect part had to be included to take into account the lack of independence among the observations. Typically, in the random effect ANOVA models adopted for the analyses, the main effects concern the effect of the overall mean of the absence/presence of KT (N-KT versus KT) and of the tempo (fast if <517.33 ms, slow otherwise). The random effect part of the ANOVA models was specified in order to separately measure the variability within individuals and within performances. Moreover, the residual variance among observations, once taken into account for the main fixed and the random effects, was further modeled to take into account possible residual heteroscedasticity.

Moreover, in order to evaluate the precision of IWFEs, we used coefficients of variation (CVs = SD / mean × 100). CVs of IWFEs durations were used to investigate whether the KT influences the precision of IWFEs performances under different conditions and, if not indicated otherwise, are to be considered as the condition's and the range's means.

Lag-one autocorrelation analysis is used as statistical signature to investigate the processes for temporal regulation. It is assumed (see: Wing and Kristofferson, 1973a, b) that series of produced time intervals regulated by the event-based process should have negative lag-one autocorrelation values (between -0.5 and 0). Conversely, emergent timing is characterized by positive lag-one autocorrelation values (between 0 and 0.5). To study the influence of KT in the Cl and Cl2 conditions we computed series of windowed lag-one autocorrelations $w\gamma(1)$ (Delignières and Torre, 2011) for each set of IWFEs. Each windowed autocorrelation coefficient was computed as the mean of a set of 30 autocorrelations. Moving the set along the sequence, a series of windowed autocorrelation coefficients was computed for each performance, measuring autoregressive linear dependency within the IWFEs. Then, we calculated the mean of the obtained windowed lag series for each performance. We considered the mean $w\gamma(1)$ as an estimator of overall dependence in the performance. Furthermore, we calculated the percentage of positive and negative windowed

$w\gamma(1)$ values for each performance. If not indicated otherwise, the mean of $w\gamma(1)$ and the percentage of positive and negative $w\gamma(1)$ are to be considered as the condition's and the range's means. To analyze the observed $w\gamma(1)$ we adopted random effect ANOVA model for repeated measurements. In order to allow an appropriate use of parametric statistical tests, the Fisher's Z-transformation was used to normalize the distribution of data (Nolte et al., 2004; Freyer et al., 2012).

4.4 Results

Timing variability

Examples of our datasets are illustrated in Figure 13 as parallel box plots, for the Mu and Mu2 conditions. It is interesting to note that pairs of N-KT - KT plots are relatively analogous when compared for slow (≥517.33 ms) or fast (<517.33 ms) movements durations. Also, it is easily appreciable that while median, upper and lower hinges and whiskers are visibly similar for pairs of N-KT - KT parallel box plots in the slow and fast collections of movements durations, the position and especially number of outside values is reduced when KT is applied, with the lonely exception of a single far out value in the condition Mu2 for slow movements with KT.

We estimated separate random effect ANOVA models for the different conditions: without audio information (Fr), with clicks (Cl) or music (Mu), and in the recall conditions (Cl2 and Mu2). The estimates for the main effects for the models in the two audio conditions Cl and Mu are reported in Table 5, together with their p-values and confidence intervals. As aforementioned, for these models the response variable is the difference between the observed and the expected IWFEs durations. As can be seen in Table 5, the overall mean is negative and significant in both models. This implies that, under a slow stimulus, observed IWFEs durations are, on mean, shorter than expected. The effect of tempo (movement duration) is significant in both Cl and Mu conditions, correcting the mean error towards zero. Conversely, KT has no significant effect on the mean error.

The parameters concerning the random effects are also of interest. These parameters specifically shape the variability of the response variable. All the parameters for the random effects reported in Table 5 are significant according to the appropriate likelihood ratio test. Remarkably, the most relevant result concerns the fact that the residual variability resulted heterogeneous between N-KT or KT cases. The KT-specific residual variances (usually called factor-specific residual variances, see: Muthén, 1989; for details on random effects model for heterogeneous population) result significantly different (Table 6). Table 6 reports the estimate of the ratio between the residual variance for N-KT and KT cases. Both in the case of Mu and of Cl stimuli, this ratio is significantly less than one, assessing that the presence of the tape significantly help to decrease the variability of the errors in IWFEs durations. In particular, residual variance for KT cases is about 14% less of the variance for N-KT cases in Cl and 8% less in Mu.

A similar model was adopted for the recalls Cl2 and Mu2, recorded 2 minutes after the audio stimuli (Table 7). In this second model, the main effects are the overall mean, the condition and the movement duration, and the absence or presence of KT. None of the estimates are significant, suggesting that, on mean, there is no evidence of a systematic error in IWFEs durations when movements are performed during recalls of music or clicks, recalls of fast or slow audio stimuli, and recalls with N-KT or KT. Interestingly, the presence of KT still helps to significantly reduce the residual variance of about 6% (Table 6). The KT residual variance ratio is estimated 0.9412 (95% confidence interval: 0.9252; 0.9575).

For the condition without audio stimulus (Fr), the model considers as the response variable directly the observed duration (Table 7). Consequently, the overall mean simply measures the mean movement duration chosen for performances of slow movements with N-KT, while the main effect of movement duration measures the increment in beats per minute implied by a faster tempo. The overall mean and the main effect of tempo are then obviously significant by construction. The main effect of KT is not significant. For this particular model, this result implies that individuals choose the tempo of the performance independently of the presence of the tape on their arm. Regarding the random part of the model, again it is worth to notice that the effect of the KT in reducing the residual variability is still significant (Table 6). The residual variance, small but still present, is about the 3% less in KT cases (estimate: 0.9708; 95% confidence interval: 0.9511; 0.9908).

The CV of IWFEs is used to normalize measures of temporal variability. We plotted the CVs of IWFEs as a function of the ranges of movement duration to visualize the rate dependent changes of the precision of isochronous performances and the interactions between these changes and the different experimental cases (N-KT or KT). The CVs of IWFEs, ranked per within-ranges of IWFEs durations, are illustrated in Figure 14 for all conditions (A-E). CVs values appear to change with movement duration. In particular, CVs of IWFEs become smaller as IWFEs become faster and, within the same condition and for the same range of movement duration, CVs values are very often smaller in KT than in N-KT cases. In Figure 14F the five within-condition CVs of IWFEs durations are compared for N-KT and KT cases. The CVs values of IWFEs are below 5% in all conditions and for both N-KT and KT cases. It is also noticeable that the within-condition CVs values are always smaller in KT, when values for the same condition are compared, and that the difference is maximal for the condition Cl. Also, in Figure 14G are shown the percent reductions for the within-condition CVs in the case of KT application. The percent reduction for the within-condition CVs values is maximal when IWFEs are performed while listening to an audio stimulus such as clicks (10.33%, for Cl). Impressively, a percent reduction for within-condition CVs values in KT is visible in all other conditions (5.47%, for Mu; 4.03%, for Cl2; 5.96%, for Mu2; and 3.50%, for Fr; see Fig 14G).

The processes for temporal regulation

To explore whether, and to what extent, the processes for temporal regulation are influenced by the application of KT, the mean wγ(1) values and the percentages of positive wγ(1) of IWFEs computed in N-KT and KT cases are compared. We plot the mean wγ(1) values and the percentages of positive wγ(1) as function of ranges of movement durations of IWFEs. As an exemplar comparison, we here describe and analyze the Cl and Cl2 conditions since we already showed them to be the most subjective to the application of KT.

The mean wγ(1) values of IWFEs ranked per within-ranges of movement durations are displayed in Figure 15 for the N-KT and KT cases of the Cl and Cl2 conditions. In all cases mean wγ(1) values appear to change with movement durations. In the N-KT case of the Cl condition (Fig. 15A) mean wγ(1) values are almost all negative with only one exception in range 5 (for this and the following references to ranges of movement durations see Table 4) whereas in the KT case of the Cl condition (Fig. 15A) mean wγ(1) values are negative for only the half of eight ranges of movement durations. The highest peaks of mean wγ(1) values are expressed within the moderato, allegro and presto tempi in the last four ranges of interval durations (Cl of N-KT) and in the last five ranges of movement durations (Cl of KT).

In the N-KT case of the Cl2 condition (Fig. 15B) mean wγ(1) values are all negative with only one exception in range 6 whereas in the KT case of the Cl2 condition (Fig. 15B) mean wγ(1) values are positive for more than half of ranges of movement durations. The highest peaks of mean wγ(1) values for the Cl2 condition are expressed within the moderato, allegro and presto tempi in the last five ranges of movement durations in both N-KT and KT cases.

The percentages of positive and negative wγ(1) values ranked per within-ranges of movement durations are displayed in Figure 16 as radar charts for the N-KT and KT cases of the Cl and Cl2 conditions. Here also, it appears evident that the percentage of positive wγ(1) values is sensitive to movement durations.

The values of wγ(1) of IWFEs in the Cl condition are mostly negative for the N-KT case (75.27% of negative values and 24.73% of positive values). In the KT case, although the amount of positive values increases, negative wγ(1) values continue to outnumber positive ones (61.43% of negative values and 38.57% of positive values). In the N-KT case of the Cl condition (Fig. 16A), percentages of positive wγ(1) values are extremely low in the first four ranges of movement durations. The highest peaks for percentages of positive wγ(1) are evident in the last four ranges of movement durations. The highest peaks for percentages of positive wγ(1) values are always less than 50%, with only one exception (range 6, 53.23%). In the KT case of the Cl condition (Fig. 16C), percentages of positive wγ(1) values are extremely low only in the first two ranges of movement durations. However, the percentages of positive wγ(1) values in the two successive ranges (3 and 4) increase from the 2.19% and 12.38% in the N-KT case to the 34.38% and 49.93% in the KT case, respectively. Also, in the last four ranges of movement durations of KT case, the percentages of positive wγ(1) values are similar to those in N-KT case.

The values of wγ(1) of IWFEs in the Cl2 condition are somewhat negative for the N-KT case (61.09% of negative values and 38.91% of positive values) while in the KT case negative wγ(1) values slightly outnumber positive ones (54.74% of negative values and 45.26% of positive values). In the N-KT case of the Cl2 condition (Fig. 16B), percentages of positive wγ(1) reach lowest values in the first and third ranges of movement durations. In the KT case of the Cl2 condition (Fig. 16D), percentages of positive wγ(1) reach extremely low values only in the first three ranges of movement durations. The highest peaks for percentages of positive wγ(1) values are in the five last ranges of movement durations both in the N-KT and KT case. It is also well perceivable that while in the N-KT case only one of the within-range percentage of positive wγ(1) values is above the 50%, in the KT case five of the eight within-range percentages of positive wγ(1) values are above the 50%.

In Figure 16E and 16F the percentages of positive wγ(1) values of N-KT versus KT cases are compared separately for the Cl and the Cl2 conditions. As illustrated, the area generated by eight ranges percentages of positive wγ(1) values is wider in the KT than in the N-KT case, both for the Cl and the Cl2 conditions. For the Cl condition, the differential percent of positive wγ(1) values is of 13.84% (calculated as difference between the percentages of positive wγ(1) of 38.57% in KT case and that of 24.73% in N-KT case). This differential percent is equivalent to an increase of 55.96% of positive wγ(1) values in the KT case (Fig. 16G). Similarly, for the Cl2 condition, the differential percent of positive wγ(1) values is of 6.34% (calculated as difference between the percentages of positive wγ(1) of 45.26% in the KT case and that of 38.91% in the N-KT case). In the Cl2 condition, the differential percent is equivalent to an increase of 16.30% of positive wγ(1) values in the KT case.

Finally, random effect ANOVA model for repeated measurements is performed for the wγ(1) values in Cl and Cl2 conditions, respectively. The model for Cl reveals a highly significant effect for the presence of KT ($F_{1,98} = 15.126$, $p < 0.001$) and tempo ($F_{1,98} = 59.62$, $p < 0.001$). The interaction between the presence of KT and tempo shows also a significant effect ($F_{1,98} = 5.05$, $p < 0.05$). The model for Cl2 fails to reveal a significant effect of presence of KT, ($F_{1,101} = 0.34$, $p > 0.05$) and tempo, ($F_{1,101} = 3.69$, $p > 0.05$). Conversely, the interaction between the presence of KT and tempo shows a significant effect ($F_{1,101} = 5.05$, $p < 0.05$). It should be remembered here that in the Cl2 condition mean within-range wγ(1) values become more positive in KT than in N-KT only for fast tempi (see, Fig. 15B).

4.5 Discussion

In this study, we examined whether the application of KT on skin is able to reduce the timing variability of repetitive rhythmic movements in healthy subjects.

Overall, our results indicate that the temporal variability of IWFEs is influenced by the application of KT. Using a task of auditory-motor integration recently developed in our laboratory (see: Bravi et al., 2014a, 2015) we demonstrate that the timing variability is reduced in the KT case, independently of the type of sensorimotor integration required from the participant to accomplish the motor performance (i.e., without audio information, with paced audio in the form of clicks or music, and in the recall conditions). Quantitatively, the reduction in the timing variability is different for the different conditions, and is greatest for the Cl and smallest for the Fr conditions. However, even though the reduction in timing variability for the Fr condition is quantitatively smaller than those estimated for the other conditions, the residual variance for KT case is about 3% less than the variance of N-KT case, which is of great importance. In fact, the residual variance evaluates the variability in the IWFEs durations when subjects are following their own tempo, which is mostly linked to the physical performance of the movement, without the effort of following or recalling a tempo proposed by others. Also, our analysis of the CVs of IWFEs show that, in general, when IWFEs are performed in presence of KT the within-condition CVs values are smaller than those obtained in the N-KT case. Here, again, the reduction in the CVs value is maximal when IWFEs are performed while listening to an audio stimulus such as clicks and minimal when performed in the Fr condition.

Our first experimental hypothesis is that KT brings about an improvement of wrist joint proprioception due to augmented afferent input via the stimulation of cutaneous mechanoreceptors. This effect would, in turn, augment the coordination of the wrist joint during the rhythmic motor performance and consequently contribute to the reduction in timing variability of the IWFEs. The type of KT application that we used allowed us to speculate about this possible effect provided by KT: indeed, since the elastic band, placed between the lateral epicondyle of the humerus and the phalanges, is applied with the wrist positioned in maximum flexion, it cannot provide a facilitation of the ascent phase of the movement by means of elastic return to the starting position. This consents us to discard the possibility that the reduction of timing variability in the KT condition is due to the dampening of gravity, but leads us towards an explanation that KT might enhance proprioceptive information provided by activating cutaneous receptors.

Proprioception consists of a combination of joint position sense, i.e., the ability to sense the position and movement of a limb in space (Aydin et al., 2001), and the sense of muscular effort and tension (Proske and Gandevia, 2009). The joint position sense is a very important contributor to joint coordination, maintenance of muscle stiffness, and to the production of natural movements for appropriate task performance (Han and Lee, 2014). It was demonstrated that the principal muscle receptor in joint position sense is the muscle spindle; however, also cutaneous receptors have become recognized as playing an important role (Proske and Gandevia, 2009). The cutaneous receptors, subserving a sense of position and movement, respond to the stretching of skin (Proske and Gandevia, 2009). As proposed by Grigg (1996), it is plausible that the application of KT induces, during the joint movement, a pressure and a stretching/deformation of the skin, thus activating cutaneous mechanoreceptors. Therefore, the mechanical effects of KT applied to skin, augmenting skin receptor output, might enhance kinesthetic and joint position sense (Simoneau et al., 1997; Halseth, 2004).

Zelaznik and Rosenbaum (2010) performed an analysis in which timing precision was measured at different locations during both the performance of tapping and circle drawing tasks. Evidences showed that the highest values of CVs during the performance of the tapping task were at a location opposite to the specified timing location, that is, the maximum of the extension point. Earlier, Semjen and Garcia-Colera (1986) also noted that, in a tapping motor performance, timing variability showed smallest values at the instructed timing location. Hence, in tapping tasks the subject is timed to a location and the timing variability is best controlled at the corresponding event (e.g., the contact with the tap key); in circle drawing the subject is not timed to a place (i.e., is not required to rely on a target location or event) but is controlling evenly the entire movement trajectory (Spencer and Zelaznik, 2003). Our experimental design is not based on a tapping task, although the IWFEs, having clear turning points that provide salient sensory information (Elliott et al., 2009), are fairly similar. The KT seemingly relieves, at least in part, from the need of a target or an event inherent with the kinematics of IWFEs. This is particularly evident in the Cl (see Fig. 14) but also in the Mu audio conditions in which movements are performed with additional sensory cues. The extra proprioceptive information provided by KT, augmenting the stability of wrist joint during the performance, could very well account for the reduction in IWFEs temporal variability that we observed as being more pronounced in our cued conditions.

In addition, we explore the possible influences of our KT on the neural processes governing the temporal regulation for production of rhythmic movements. The mean $w\gamma(1)$ values and the percentages of positive $w\gamma(1)$ of IWFEs, calculated in N-KT and KT cases, and compared for the exemplar Cl and Cl2 conditions, show that the processes for temporal regulation can be influenced by the application of KT. We demonstrate that the mean $w\gamma(1)$ and percentages of positive $w\gamma(1)$ are in fact biased toward values congruent with the emergent mode for control of timing.

Overall, these results have important implications for the event-emergent timing distinction. Heretofore, it was suggested that a task is controlled via event timing or via emergent timing depending on the kinematic of the performed movement (Zelaznik and Rosenbaum, 2010). Huys et al. (2008) using a rhythmic motor task, such as tapping, have demonstrated that discrete and continuous movements are two classes of movements topologically distinct. Indeed, it was shown that when finger flexion-extensions are performed as slow and discrete movements, the engagement of an explicit timing (event-based) process is required; whereas when the tapping is performed as rapid and smooth movements, the employment of a self-organized limit-cycle (emergent) process is necessary. The clarity with which such events are delineated in a particular experimental situation is considered to be the factor determining the weight of the event-based timing component. The continuity of the movement largely determines the strength of emergent timing component (Repp and Steinman, 2010). In addition, in a timing study on air finger tapping, participants performed discrete movements, being instructed to pause before each flexion cycle, and continuous movements, being instructed to move as smoothly as possible without pausing (Spencer et al., 2007). Despite the subtle difference between these discrete and continuous movements, activation in the cerebellum was greater when participants were instructed to perform discrete movements, suggesting that the engagement of the cerebellum may depend on how movements are produced or, even better, on how they are represented (Spencer et al., 2007).

Our experimental hypothesis is that the application of KT, by stabilization of the motor effector during the performance, causes the IWFEs to be less discrete and thus more continuous. According to the dichotomic view of the event-based versus emergent modes of temporal control (Delignières and Torre, 2011), KT could promote the involvement of emergent timing control and, consequently, reduce the contribution of event-based timing. As a consequence, the control for timing would no longer need to refer to a nervous structure such as, for example, the cerebellum, in the building of an abstract representation of the time intervals to produce. Rather, the dynamics of the system could be sufficient per se to keep the movement cycle constant.

We demonstrate a reduction in timing variability with KT, as seen by the CVs values and their dispersion, being very often smaller in the KT than in the N-KT cases (see: Fig. 13 and Fig. 14). Such reduction seemingly suggests a transition toward an emergent timing control. This emergence of the emergent timing strategy (see: Fig. 15, and E-G in Fig. 16) appears to be by virtue of the KT to render movements less audio sensitive or dependent (compare, in Fig. 16, A to C versus B to D). This mechanism ultimately results in a reduced variability and thus, in a better - more homogenous - performance. The same concept is analogous to a computer that allocates memory for a better performance; so do the cortical and subcortical circuits, which are usually required to bear the load of motor control and of other cognitive activities. Being less dependent on external / discrete events, central structures are partially relieved from timing control, thus freeing resources and allowing for a net augmentation of the central efficiency for motor control and cognition.

In conclusion, KT was used in this study as a tool to possibly augment the precision of rhythmic movements. Our results show that KT does, in fact, reduce the timing variability of rhythmic movements performed with no direct surface opposition and minimizing visual information. In particular, our results suggest that KT - on the one hand by providing extra proprioceptive information, and on the other hand by relieving, at least partially, the central structures from time control - allows for a net augmentation of the central efficiency for motor control.

Chapter 5: Experiment IV

Exploration of Direction and Tension Effect of Kinesio Taping on Sensorimotor Synchronization. A Randomized Deceptive Trial on Healthy Adults

5.1 Abstract

In the Experiment III we found that Kinesio® Tex taping (KT) improves timing consistency of IWFEs. The present study investigates whether KT applied with different direction and tension may influence differently the precision of sensorimotor synchronization, defined as the ability to coordinate actions with predictable external events. Ten healthy participants performed sets of IWFEs synchronized to series of audio stimuli with IOI of 500 and 400 ms. IWFEs were performed with no surface opposition and visual information. KT was applied over the wrist and fingers extensor muscles. Two facilitatory (light and moderate tension) and one inhibitory applications were used in different sessions. Standard deviation of the asynchrony (SDasy), and percentage difference of SDasy were calculated and compared across KT and the control no KT cases. Different direction and tension of KT application did not influence differently the ability to coordinate rhythmic movements to an external auditory stimulus. However, compared with the control no KT case, SDasy decreased significantly in all KT cases in both 500 and 400 ms IOI, with improvements ranging between 8% and 13%. KT increases greatly - independently from direction/tension - the precision of sensorimotor synchronization and cancels the differences between conditions implicating slower and faster movements. KT method should be tested on sensorimotor disorders to check for the regaining of effective motor control.

5.2 Introduction

Kinesio® Tex taping (KT) is a kinesthetic method based on an elastic cotton strip with an acrylic adhesive developed by Japanese chiropractor, Dr. Kenso Kase, in the 1970's (Kase et al., 2003). KT is commonly used in clinical practice for treating athletic injuries and a variety of physical disorders (Morris et al., 2013). Studies report that KT application leads to improvements in a variety of musculo-skeletal conditions such as pain, reduction of range of motion, strength, and of muscle activity, as well as proprioceptive alterations (Kalron and Bar-Sela, 2013). However, the direct benefits of KT from a clinical perspective remain controversial due to inconsistent results and/or methodological limitations (Williams et al., 2012; Kamper et al., 2013).

To date one of the more debated issues regarding KT is its technique of application (Vercelli et al., 2012; Guner et al., 2015; Cai et al., 2015). KT is used in different ways in terms of tension and the direction of application. KT is believed to facilitate through recruitment of target muscle fibers (when applied from origin to insertion with light and moderate tensions, 25% and 50% respectively) or inhibit through relaxation of target muscle (when applied from insertion to origin with light 25% tension; Kase et al., 2003).

Recent works on facilitatory/inhibitory potential of KT evaluated its effect on muscle strength and obtained mixed results (Vercelli et al., 2012; Guner et al., 2015; Cai et al., 2015). In two of these studies (Vercelli et al., 2012; Cai et al., 2015) no differences were found between facilitatory and inhibitory KT cases, but also among tapeless or sham and KT cases. Besides, application instructions not followed properly may lead to unpredictable results. For instance, Cai and colleagues (2015) reported no significant differences in the maximum grip strength and electromyographic activity between facilitory and inhibitory applications; yet, KT was applied with 75% of its maximal length tension, unlike recommended by Kase (2003; see above). Moreover, even in studies in which recommendations for KT application are followed, often are used tapes different from Kinesio$^{®}$ Tex Tape, having possibly different properties (Alexander et al., 2008, Cools et al., 2002).

We have previously tested the effect of KT application on the performance of repetitive IWFEs, in a combined task of audio synchronization and recall-motor integration (Experiment III, Bravi et al., 2014b). We found that KT improves performance by reducing the temporal variability of repetitive movements, and speculated that the augmented timing consistency was due to an improvement of wrist joint coordination. A subsequent study by Pamuk and Yucesoy (2015) showed, via MRI analyses, that KT provides various directions and amplitudes of skin deformation. Local deformations of the underlying muscle tissues, both immediately targeted and distant, were also found (Pamuk and Yucesoy, 2015).

The aim of present study is to investigate the impact of different KT application techniques on the precision of sensorimotor synchronization, defined as the ability to coordinate actions with predictable external events (Repp and Su, 2013). In particular, we examine whether KT applied with different direction and tensions may influence differently our sensorimotor task.

Since it is recognized that muscle recruitment is closely related to the global functional improvement of the hand motion (Xu et al., 2015), we hypothesized that the facilitatory application of KT, by promoting the recruitment of muscle fibers and consequently stabilizing the wrist joint, would increase the precision of synchronized movements. Conversely, the KT inhibitory application, by relaxing muscle, would decrease the precision of performance.

We performed an experiment in which healthy participants, tested with different KT applications and without KT, executed, in separated sessions, sets of repeated IWFEs in synchrony with streams of clicks.

5.3 Methods

Participants

Ten healthy adults were enrolled for this study (age: 26.2 ± 3.9 years; 6 males and 4 females). According to the laterality score from the Edinburgh Handedness Inventory (Oldfield, 1971) all participants except one (-60.0, left handed) were right handed (87.0±10.0). Participants were naive to the purpose of the study and they knew nothing about the KT method. In addition, they were no musically trained, and all reported no auditory, motor, or other neurological impairments. Experimental procedures conformed to the declaration of Helsinki and were approved by the local Ethics Committee (Comitato Etico Area Vasta Centro AOUCareggi, Florence, Italy). Written informed consent was obtained from all participants.

Set up

The setup is fully described elsewhere (Bravi et al., 2014a; 2014b; 2015) and is here summarized.

Each participant was tested individually, sitting upright on a chair with the feet on leg rest, wearing eye mask (to prevent interference from visual information) and headphones (to reduce environmental noise and to deliver audio information; K 240 Studio, AKG Acoustics GmbH, Wien, AT). The participant's dominant forearm was placed on armrest, in a relaxed horizontal position. The wrist and hand of the participant were free to move in mid-air with no direct opposition, thus minimizing tactile information. A triaxial accelerometer (ADXL330, Analog Devices Inc., Norwood, MA, USA) was placed on the dorsal aspect of hand, over the proximal part of the 2nd–3rd metacarpal bones (Fig. 17A). Sensor output was acquired and digitized at 200 Hz through PCI-6071E (12-Bit E Series Multifunction DAQ, National Instruments, Austin, TX, USA). Streams of clicks of 60 s duration were produced using Audacity®, via the Generate Click Track function. The audio files were constructed as a series of 20 ms sounds, set to white noise, followed by 480 ms of silence for the IOI of 500 ms or by 380 ms of silence for IOI of 400 ms.

For the KT (Kinesio® Tex Gold™ FP-2″ Red) application the participant, already seated on the chair with forearm in full pronation and rested on the armrest, was asked to keep the wrist in full flexion. KT was applied, according to a protocol previously reported (Experiment III, Bravi et al., 2014b), from the lateral epicondyle of the humerus, in a wave-like pattern, over the extrinsic extensor muscles of the hand, to the metacarpal area and fingers following the course of the tendons. In the facilitatory KT cases, KT was applied from origin to insertion with two different length tensions: light and moderate (fKT and fKT-T, 25% and 50%, Fig. 17B and C, respectively). In the inhibitory KT case (iKT, Fig. 17D), while the KT contact area was identical with those of the facilitatory KT applications, the direction was reversed (i.e., KT was applied from insertion to origin). In this latter case KT was applied with a light length tension of 25% (Kase et al., 2003). The tensions of KT were assessed according to the method described in Kase (2003). KT was applied in all participants by the same investigator (Pelosin et al., 2013).

Sessions

Each participant had participated in four sessions (three with KT and one without KT, i.e., the N-KT case) that were performed at least at a three days' distance. The order of the four sessions was randomized between participants. Every session was performed with the dominant hand. In all sessions the participant was instructed to perform sets of repetitive IWFEs while listening to clicks at a similar pace concurrently with the tempo of the audio (i.e., maintaining an in-phase 1:1 relationship between repeated wrist's flexion-extensions and the tempo of the audio). Each session consisted of 16 sets of repeated IWFEs, 8 synchronized to streams of clicks with 500 ms IOI and 8 to streams with 400 ms IOI; 45 s rests separated the sets of IWFEs to avoid fatigue during performance (Fig. 17E). The order in which the clicks at 500 or 400 ms were presented was set to obtain equivalent number of participants that received first one IOI or the other. The KT sessions started 10 min after mounting the tape to overcome perception of tape on the skin (Kase et al., 2013). At end of each KT session participants removed the KT.

Data Format

Kinematic parameters were evaluated from a total of 640 sets of movements (64 sets per participant). Data from the sensor were stored and an off-line analysis of raw data from the triaxial accelerometer was implemented. The signal extracted from the accelerometer presented a minimum when the wrist reached the maximum flexion and a maximum when it reached the maximum extension. The duration of a single wrist's flexion-extension (i.e., IWFE duration) was calculated as the distance between two consecutive flexion-extension minima (custom software developed in Matlab®).

Statistical Methods

To investigate whether different KT applications are able to influence differently the precision of synchronized IWFEs, we used standard deviation of the asynchrony (SDasy), a measure of sensorimotor synchronization precision, which is used to evaluate coupling-strength between the movement and auditory signal (van der Steen et al., 2014). A lower SDasy reflects a stronger coupling between the pacing auditory markers and the participant's movements.

Percentage difference o Δ% of SDasy [($SDasy_{KT}$*100)/ $SDasy_{N\text{-}KT}$] was calculated to measure percentage differences between every single case in which KT was applied (fKT, fKT-T, and iKT) and the case in which KT was not applied (N-KT). SDasy and Δ% of SDasy are to be considered as the case's means.

Separate one-way ANOVA analyses were conducted on absolute values of SDasy to evaluate within-case differences. The factor considered in all ANOVA was the case (i.e., N-KT, fKT, fKT-T, iKT). To take into account for multiple testing, ANOVA analyses were followed by Bonferroni post-hoc correction. We fixed the significance level at 0.05.

Since we were interested in the synchronization performance under the best of conditions, we compute the analyses and report results for the best six sets (in terms of the smallest SDasy) out of the eight performed, for each participant within each IOI condition (Zelaznik and Rosenbaum, 2010).

5.4 Results

For the 500 ms IOI, absolute values of SDasy are remarkably different between N-KT (13.09 ms) and the other KT cases (fKT = 11.97 ms; fKT-T = 11.58 ms; iKT = 11.37 ms; Fig. 18A) with an improvement of precision of synchronization in KT cases ranging between 8.5% and 13% (Fig. 18B). Also for the 400 ms IOI, absolute values of SDasy are different between N-KT (11.12 ms) and the other KT cases (fKT = 10.21 ms; fKT-T = 10.23 ms; iKT = 9.73 ms; Fig. 18C) with an enhancement of precision in KT cases ranging between 8% and 12.5% (Fig. 18D).

One-way ANOVA analyses of SDasy values performed on N-KT, fKT, fKT-T, and iKT, for the IOI of 500 and 400 ms, show highly significant differences

($F_{3,236} = 9.071$, $p < 0.001$, and $F_{3,236} = 7.870$, $p < 0.001$, respectively). Bonferroni post-hoc tests among groups, for both the IOI of 500 and 400 ms, show highly significant differences between N-KT and all KT cases (all $p < 0.01$), but no significant differences between the different KT cases (fKT and iKT, $p > 0.05$; fKT and fKT-T, $p > 0.05$; fKT-T and iKT, $p > 0.05$), substantiating that SDasy is influenced by KT, but that it is not influenced differently by direction or tension of the application. Finally, one-way ANOVA analysis of SDasy performed on N-KT, fKT, fKT-T, iKT of 500 ms IOI, and N-KT of the 400 ms IOI show highly significant differences ($F_{4,295} = 9.772$, $p < 0.001$). Bonferroni post-hoc tests show highly significant differences between N-KT of 500 ms IOI and N-KT of 400 ms IOI ($p < 0.001$), but no significant differences between the different KT cases (fKT, fKT-T, iKT) of 500 ms IOI, and the N-KT of 400 ms IOI ($p > 0.05$).

5.5 Discussion

The purpose of the study was to determine whether different techniques of KT application influence differently the precision of a synchronized rhythmic performance. Our results show that the facilitatory and inhibitory KT applications do not influence differently such ability.

As already mentioned, mixed results were obtained in studies evaluating the facilitatory/inhibitory potential effect of KT. For instance, Vercelli reported no significant effect in the maximal quadriceps strength immediately after the inhibitory, facilitatory, or sham KT applications (Vercelli et al., 2012). Conversely, Guner showed that facilitatory KT application affected the terminal stance phase and that inhibitory KT influenced the terminal swing phase compared with the tapeless condition (Guner et al., 2015).

Our data, even if achieved with a task extremely different from the more common tasks of muscle strength, are in accord with those of studies in which no differences between KT applications with different direction were found (Vercelli et al., 2012; Cai et al., 2015; Cools et al., 2002). Indeed, although the most improved synchronization is obtained when applying the KT with inhibitory technique, no significant differences are evidenced between inhibitory and facilitatory KT cases.

In addition, the KT tape tension does not influence the ability to synchronize movements to an auditory stimulus. Pamuk and Yucesoy (2015) show, via MRI analyses, that KT application may have widespread heterogeneous deformation effects on the skin as well as on the underlying and deeper muscle tissues, ascribing the result to the intimate connection between muscular and connective tissues (Pamuk and Yucesoy, 2015). They finally propose to evaluate whether KT applications with different tension could cause different effects. We cannot exclude the presence of different deformation patterns when KT is applied with different tension, yet we provide evidence that different tension of KT application do not have a different impact on the synchronization performance.

Moreover, our results, besides confirming previous data (Bravi et al., 2014b), show that KT improves - independently from direction/tension - the ability to synchronize rhythmic movements to an external auditory stimulus.

In the previous study (Bravi et al., 2014b) we attributed the KT-dependent improvement of timing precision to an extra-proprioceptive effect by activation of cutaneous mechanoreceptors via stretching/deformation of skin (Grigg, 1994). The recent demonstration of deformations of targeted and deeper muscle tissues caused by KT application (Pamuk and Yucesoy, 2015), permits to speculate that also muscle spindles may be stimulated by KT during the movement since local deformation have an effect on such receptors (Prochazka and Ellaway, 2012). Muscle spindles, as well as skin stretch receptors, play a key role in sense of position and of movement, which is critical to perform precise movements (Walsh et al., 2013). Thus, it is plausible that during the wrist flexion period, when deformation of the skin and underlying extensor muscles occurs, the extra stimulation of proprioceptors by KT leads to an augmented sense of position and an enhanced recruitment for the fibers of wrist and fingers extensor muscles working in eccentric mode. Specifically, the stimulation of primary sensory endings of spindles, sensitive to velocity of stretch, may favor the generation of rapid responses to answer unexpected variations of muscle length along the flexion trajectory (Prochazka and Ellaway, 2012). The result is an augmented control of the wrist's descending phase that may favor the coordination between flexion movement and the auditory stimulus, especially in a repetitive task in which fatigue may reduce motor control and the precision of the movement (Zhang et al., 2015).

Furthermore, KT's effectiveness is high to such an extent that participants performing with KT slower movements (500 ms IOI) are brought to the level of precision reached in performances of faster movements (400 ms IOI) without KT. Movement frequency is a critical factor able to influence human synchronization skills. Additionally, the precision of synchronized movements depends highly on the experimental context (e.g., sensory modality, sensorimotor pattern). Previous studies, using a flex-on the beat motor task, showed that lengthening the temporal interval increased SDasy (Repp, 2003; Lorås et al., 2012). Our results are compatible with these studies (SDasy is always greater for IOI of 500 ms than for IOI of 400 ms). When augmenting the required rate of movement, more robust intrinsic synergies are expressed by reciprocal activation of the flexors and extensors muscles (Li et al., 2004) with a concomitant enhancement of the sensorimotor cortex activity (Blinkenberg et al., 1996). Consequently, a more efficient joint stability during movements is available, leading to an augmented precision of synchronized movements. It is acknowledged that control strategies of the human movement are constrained by the neuroanatomical characteristics of the motor systems (Carroll et al., 2001). Our results suggest that KT effect is associated with variations in the nature of the neuro-anatomical constraints determining the control of voluntary movement.

5.6 Conclusions

KT applied over the wrist and fingers extensor muscles with different direction and tension did not influence differently the precision of a synchronized rhythmic performance. However KT, possibly by improving the efficiency of motor control strategies, greatly increases the precision performance of our sensorimotor coordination task and cancels the differences of synchronization precision between conditions implicating slower and faster movements. KT applications should be tested on sensorimotor disorders like the musician's dystonia to check for the regaining of effective motor control.

Chapter 6: Experiment V

The Impact of Kinesio Taping on Dominant and Non-dominant Hands

6.1 Abstract

In the Experiment III we have demonstrated that KT improves significantly the precision of IWFEs in terms of isochrony (timing consistency). Motor behavioral research has shown numerous preferred arm advantages in the generation of motor output including increases in the strength, speed and consistency of movement. Therefore, supposing that differences in terms of timing variability between dominant and non-dominant hands would be revealed, in this study we investigated whether KT is able to counterbalance the expected difference of timing precision between the two hands. Twenty-two healthy subjects, tested with and without KT, have participated in two sessions (KT and N-KT cases) in which sets of IWFEs were performed in a task of synchronization-continuation. Kinematics was recorded and temporal parameters were extracted and analyzed. We studied two time conditions (800 and 550 ms). Differently from what we expected, no differences were found between the dominant and non-dominant hands when IWFEs were performed in N-KT cases. In addition, KT was not able to influence timing consistency of IWFEs having time interval longer (800 ms); on the contrary, KT improved the timing consistency of IWFEs having temporal interval of 550 ms. In particular, in this last time condition was found an asymmetric effect of KT when applied on different motor effectors. Finally, correlating studying whether different level of timing skills, as expressed by the time consistency, influences the neural processes governing the temporal regulation for production of rhythmic movements. A finally investigation was performed on the two forms of time control, event-based timing and emergent timing, showing that the amount by which a timing mechanism is activated is correlated with the efficiency of the subject to be in time.

6.2 Introduction

The tendency for humans to prefer the use of one arm versus the other, when performing activities of daily living, has been cited as one of the most evident examples of lateralized brain function (Goble, 2006). Despite the enduring nature of right arm preference, no consensus has been reached regarding its origin.

Various theories have been proposed to explain the origin of arm preference, yet no unanimous consensus has been reached regarding its origin. One of the foremost genetic theories is the "right shift theory" of Annett (1972), grounded in Mendelian genetics, proposing that one allele (RS+) leads to the development of both arm and language abilities in the left cerebral hemisphere, and a second allele (RS-) allows for arm praxis and language abilities to be randomly distributed in either hemisphere (Annett, 1998; Goble, 2008b). However, It was argued that environmental and socio-cultural factors are influencing the handedness. Indeed, it is reported that many natural left-handers have been forced to adopt right-arm preference to avoid religious and social stigmas associated with left-handedness or "sinistrality" (Coren, 1993; Harris, 1990).

Motor behavioral research has revealed numerous preferred arm advantages in the generation of motor output including increases in the strength, speed and consistency of movement (Goble and Brown, 2008). For instance, Armstrong and Oldham (1999) showed that healthy subjects with the preferred arm produce forces approximately larger by 10% than those produced with the non-preferred arm (Armstrong and Oldham, 1999). Morever, numerous finger tapping experiments have demonstrated clearly that timing consistency and rate of movement differentiate between the preferred and non-preferred hands:

specifically, preferred arm advantages in the speed and timing consistency were shown (Peters and Durding, 1979; Todor et al., 1983; Schmidt et al. 2000).

On the basis of these findings it is likely to assume that differences in terms of timing variability will be likewise shown between IWFEs performed with preferred and non-preferred hand. The first aim of this study is then to evaluate whether KT is able to counterbalance the expected difference of timing variability between the dominant and non-dominant hand.

In addition, we studied whether different level of timing skills influences the neural processes governing the temporal regulation for production of rhythmic movements

6.3 Methods

Partecipants

A total of twenty-two healthy adults were enrolled for this study (age: 22.4 ± 3.2 years; 9 males and 13 females). According to the laterality score from the Edinburgh Handedness Inventory (Oldfield, 1971) all participants were right handed (82.63±23.0). Participants were naive to the purpose of the study and they knew nothing about the KT method. In addition, they were no musically trained, and all reported no auditory, motor, or other neurological impairments. Experimental procedures conformed to the declaration of Helsinki and were approved by the local Ethics Committee (Comitato Etico Area Vasta Centro AOUCareggi, Florence, Italy). Written informed consent was obtained from all participants.

Set up

The experimental setup is largely that used in the Experiment IV, so here will be summarized briefly.

Each participant was tested individually, sitting upright on a chair with the feet on leg rest, wearing headphones (to reduce environmental noise and to deliver audio information; K 240 Studio, AKG Acoustics GmbH, Wien, AT). The participant's dominant forearm was placed on armrest, in a relaxed horizontal position. The wrist and hand of the participant were free to move in mid-air with no direct opposition, thus minimizing tactile information. A triaxial accelerometer (ADXL330, Analog Devices Inc., Norwood, MA, USA) was placed on the dorsal aspect of hand, over the proximal part of the 2nd–3rd metacarpal bones. Sensor output was acquired and digitized at 200 Hz through PCI-6071E (12-Bit E Series Multifunction DAQ, National Instruments, Austin, TX, USA).

Streams of 16 clicks were produced using the audio editor Audacity (GNU/GPL, http://audacity.sourceforge.net/), via the function Generate Click. The audio files were constructed as a series of 20 ms sounds, set to white noise, followed by 530 ms of silence for the IOI of 550 ms or by 780 ms of silence for IOI of 800 ms.

For the KT (Kinesio® Tex Gold™ FP-2″ Red) application the participant, already seated on the chair with forearm in full pronation and rested on the armrest, was asked to keep the wrist in full flexion. KT was applied with a moderate length tension of 50% (fKT-T; Kase et al., 2003). The tension of KT was determined according to the method described in Kase (2003). KT was applied in all participants by the same investigator (Pelosin et al., 2013). KT was applied, according to a protocol previously reported in the Experiment III.

Data Format

Data format is that used in all experiments described previously.

Sessions

Each subject had participated in two sessions, one with no KT (N-KT), one with KT that were performed at least at a three days' distance. The KT session started approximately 10 minutes after mounting the tape since this interval is needed to overcome perception of tape on the skin (Kase et al., 2013). The order of the two sessions was randomized between participants.

In the reproduction task, the metronome produced 16 beats and then turned off. Participants entrained to the metronome, attempting to complete a cycle coincident with the beat of the metronome (i.e., maintaining an in-phase 1:1 relationship between repeated wrist's flexion-extensions and the tempo of the audio; paced phase). When the metronome turned off the participants attempted to produce movements with the same time interval for approximately one minute (unpaced phase).

In each session IWFEs sets were performed with dominant and non-dominant hand, before with one and later with the other hand. A total of 32 sets of IWFEs were performed in each session, whose 16 sets with each hand. Eight sets were performed unimanually at each of two interval duration conditions (550 and 800 ms; Fig. 19). The order of hands with which to perform IWFEs and interval duration was randomized. The KT sessions started 10 min after mounting the tape to overcome perception of tape on the skin (Kase et al., 2013). At end of each KT session participants removed the KT.

Only the data from the unpaced phase were analysed. The first two IWFEs of the unpaced phase were discarded and the analyses were performed on the remaining IWFEs (Harrington et al., 2004)

Statistical Methods

We calculate the CV (CV = SD * 100 / mean) of IWFEs durations to assess the timing variability (precision) of IWFEs performances in N-KT and KT cases. Δ% of CVs was calculated to measure percentage differences of CVs between N-KT and KT cases (see above, Experiment IV, for the computation of Δ%).

Also we use to correlate mean CV values expressed in increasing order of magnitude, and obtained by each subject in N-KT case, with the respective Δ% of CVs value, to evaluate whether the effect of KT is related to the level of timing efficiency.

Moreover, series of (windowed) lag-one autocorrelations, herein abbreviated wγ(1), were performed for each set of IWFEs to explore whether KT influence timing control processes (see Experiments II and III). Δ% of wγ(1) was calculated to measure percentage differences of wγ(1) between N-KT and KT cases (see Experiment IV for the computation of Δ%).

Finally, correlating mean CV values expressed in increasing order of magnitude, and obtained by each subject in N-KT case, with the own mean wγ(1) value, we evaluate whether a relationship exists between the level of timing efficiency and the type of timing strategy employed to perform IWFEs.

6.4 Results

6.4.1 Dominant Hand

The mean time interval (accuracy) was calculated before the CVs of IWFEs, for both 800 and 550 ms conditions. Such parameter reflects the extent to which subjects achieved the standard interval. It allows us to exclude that CV differences between groups are related to the tempo differences of IWFEs performed in each case. On average, participants were accurated to reproduce the required time interval for both conditions, in N-KT and KT cases (Fig. 20A, B).

In the 800 ms condition, no differences between CVs values of N-KT and KT cases are found (4.65% and 4.55%, respectively; Fig. 21A). An irrelevant improvement of the temporal precision obtained by KT is shown (≈ 2%; Fig. 21B). For the 550 ms condition, differences between CVs of N-KT and KT cases are found (3.69% and 3.47%, respectively; Fig. 21C). An improvement of the temporal precision obtained by KT is shown (≈ 6%; Fig. 21D).

Finally, in both 800 and 550 ms conditions, when correlating mean CVs values obtained by each subject in N-KT case with the respective Δ% of CVs, it has shown that KT has a greater effect when the subject performs IWFEs with higher temporal variability in N-KT case; conversely, KT worsens the timing performance in subjects with lower temporal variability (Fig. 22A, B).

Windowed Lag-one Autocorrelation

In the 800 ms condition, the mean wγ(1) was positive in N-KT and KT cases (0.15±0.13 and 0.11±0.14, respectively; Fig. 23A), with a reduction of the employment of the emergent timing component (≈ -27%) when KT is applied; Fig. 23B). For the 550 ms condition, wγ(1) values were strikingly positive in N-KT and KT cases (0.28±0.15 and 0.34±0.14; Fig. 23C), with an augmented employment of the emergent timing component when KT is applied (23%; Fig. 23D). In N-KT cases, the mean wγ(1) value of IWFEs with a time interval of 800 ms is lower than mean wγ(1) value of IWFEs with a time interval of 550 ms.

Finally, in the N-KT case for both 800 and 550 ms conditions, when timing performance presents a low temporal variability, the mean value of wγ(1) tend to be remarkably positive (Fig. 24A, B). The higher is the temporal variability of IWFEs, the more the mean wγ(1) positive value is reduced, until reaching negative values in the 800 ms condition (Fig. 24A).

6.4.2 Non-dominant Hand

The mean time interval was calculated before the CVs of IWFEs, for both 800 and 550 ms conditions. On average, participants were equally accurated to reproduce the required time interval for both conditions, in N-KT and KT cases (Fig 25A, B).

In the 800 ms condition, no differences between CVs values of N-KT and KT cases are found (4.40% and 4.39%, respectively; Fig. 26A, B). Conversely, in the 550 ms condition, differences between CVs of N-KT and KT cases are found (3.86% and 3.40%, respectively; Fig. 26C). A remarkably improvement of the temporal precision achieved by KT is shown (≈ 12%; Fig. 26D). Such improvement is doubled respect to when IWFEs are performed with the dominant hand.

Furthermore, as already shown for the dominant hand, in both 800 and 550 ms conditions, when correlating mean CVs values obtained by each subject in N-KT case with the respective Δ% of CVs, it has shown that KT has a greater effect when the subject performs IWFEs with higher temporal variability in N-KT case; contrary, KT worsens the timing performance in subjects with lower variability (Fig. 27A, B). Finally, it is possible to observe that the effect of KT is greater, the more the subjects'timing performance in the N- KT condition presents high CV.

Windowed Lag-one Autocorrelation

In the 800 ms condition, the mean $w\gamma(1)$ was positive for N-KT and KT (0.17±0.13 and 0.15±0.13, respectively; Fig. 28A), with a reduction of the employment of the emergent timing component (≈ -10%) when KT is applied; Fig. 28B). For the 550 ms condition, $w\gamma(1)$ values were strikingly positive in N-KT and KT cases (0.26±0.14 and 0.33±0.13; Fig. 28C), with an augmented employment of the emergent timing component when KT is applied (≈ 29%; Fig. 28D). Finally, in N-KT cases, the mean $w\gamma(1)$ value of IWFEs with a time interval of 800 ms is lower than mean $w\gamma(1)$ value of IWFEs with a time interval of 550 ms.

Finally, in N-KT case for both 800 and 550 ms conditions, when timing performance presents a low temporal variability, the mean value of $w\gamma(1)$ tend to be remarkably positive (Fig. 29A, B). The higher is the temporal variability of IWFEs, the more the mean $w\gamma(1)$ positive value is reduced, until reaching negative values in the 800 ms condition (Fig. 29A).

6.5 Discussion

Working on the hypothesis that timing variability differences would be shown when IWFEs are performed with the dominant and the non-dominant hands, the first aim of this study was to investigate whether KT is to able to neutralize such differences between the two hands. Differently from what we expected, no differences were found between the dominant and non-dominant hands in terms of timing variability when IWFEs were performed in N-KT cases. These results are in contrast with those of several studies that have dealt with exploring timing skills' asymmetries between preferred and non-preferred hands (Peters and Durding, 1979; Todor et al., 1982; Schmidt et al., 2000). For instance, Schmidt and colleagues, studying the effects of gender and handwriting preference on manual asymmetry in tapping rate and intertap variability, showed that right-handers presented greater manual asymmetries than left-handers for both tapping rate and intertap variability. In addition, right handers exhibited a significant greater asymmetry for intertap variability than tapping rate (Schmidt et al., 2000). Although studies of motor output have provided valuable insight regarding asymmetries in upper limb performance, our results cannot confirmed them in terms of timing consistency. Differences in data can be accounted to high speed tapping and short duration of sets of movements (10 s) performed in these studies.

In general, our data show that KT is not able to influence the precision of IWFEs having a time interval of 800 ms. Contrary, KT improves the timing consistency of IWFEs with 550 ms interval duration. Specifically for IWFEs with 550 ms interval duration, a different effect of KT is found when IWFEs are performed with different hands, with a greater effect of KT achieved when applied on the non-dominant hand.

Therefore, our results show an asymmetric effect of KT on the timing consistency of IWFEs when performed with different motor effectors. We speculate that whether KT is able to modulate proprioception system, it could influence differently the timing consistency of IWFEs performed with different motor effectors. Indeed, it is suggested that each hemisphere may rely on sensory feedback to a different degree for the achievement of goal-directed movement (Goble et al., 2006). Specifically, the non-preferred arm/hemisphere system was shown to be more adept for the processing of proprioceptive information (closed loop) than preferred arm/hemisphere system. Indeed, preferred arm/hemisphere system is suggested more likely to function in a feedforward (open-loop) fashion (Goble and Brown, 2007).

This asymmetry between upper limbs in the employment of proprioceptive feedback likely arises from functional differences in the roles of the preferred and non-preferred hands during bimanual tasks (Han et al., 2013).

One of the most important sources of movement-related feedback is proprioceptive information from muscle, joint and skin receptors (Goble and Brown, 2007). Thus, it is plausible that KT, by modulating proprioception information, influences mostly the precision of IWFEs when performed with the non-dominant hand since stimulating a system more dependent on the online utilization of sensory feedback (closed-loop) mechanisms (Goble and Brown, 2007).

Moreover, our data show that the effect of KT in improving the precision of rhythmic performance is greater the more variable are IWFEs in the N-KT case. There is the assumption that the ability to generate and utilize proprioception information in healthy adults varies with their skill level of motor control (Muaidi et al., 2009). Muaidi and colleagues have shown that highly trained soccer players possess enhanced proprioceptive acuity that may be developed as a result of long-term athletic training (Muaidi et al., 2009). Also, Lin and colleagues (2006) found that elite tennis players possess proprioceptive acuity significantly better than that of amateur and novice players. Thus, a more efficient ability to manage proprioception is acquired for an elite performance. We speculate that subjects that produce IWFEs with a higher timing variability may have reduced efficiency of the proprioceptive system, and therefore are more sensitive to this sensorial support induced by KT. Hence, it is possible to say "The less you are precise the more Kinesio taping helps you".

Furthermore, a symmetric effect of KT in influencing the timing strategies employed for IWFEs was found. However, while for IWFEs with 800 ms inteval duration KT application tends to reduce the emergent timing elicitation (in particular on the dominant hand), for IWFEs with 550 ms inteval duration KT increases the exploitation of emergent strategy. Also, the frequency of IWFEs influence the timing strategy (Huys et al., 2008; Bravi et al., 2015) since, at high frequency, the oscillatory nature of movement increases the exploitation of emergent control. For this reason, mean $w\gamma(1)$ values of IWFEs with shorter duration (550 ms) are higher than those of IWFEs with longer duration (800 ms).

Finally, we explored whether different levels of timing skills influence the neural processes governing the temporal regulation for production of rhythmic movements. In the N-KT case, and for each participant, mean CV values expressed in increasing order of magnitude are correlated with mean $w\gamma(1)$ values. We noticed that the employment of emergent timing is related to the level of consistency of timing performance. Previously, it has been shown that, in a task where tactile information is minimized, either the event-based or the emergent timing strategy are elicited in exclusively alternation way (Experiment II). Here, it is shown, for both hands, that individuals performing rhythmic movements with low temporal variability mostly employed the emergent timing mode; vice versa, individuals performing repetitive movements with high temporal variability reduce steadily the engagement of emergent strategy, until to use also the event-based timing in some cases (evident for movements with 800 ms time interval).

It has demonstrated that discrete and continuous movements are two classes of movements topologically distinct. Indeed, it was shown that when repetetive movements are performed as slow and discrete actions, the engagement of a neural structure, or a network of structures, not implicated in the implementation of the dynamics for motion is required (event-based timing); whereas when the actions are performed as rapid and smooth movements, the employment of a self-organized limit-cycle process is necessary (emergent timing; Huys et al., 2008).

It is possible to speculate that individuals with lower temporal variability, feeling themselves to fit well with the task due to a more efficiency of sensorimotor processes, perform fluid and continuous IWFEs in automatic way, exploiting an emergent-low level timing. Conversely, it plausible that individuals endowing with less control of motor effector perform sequence of discrete movements controlled more at cognitive level.

Lewis and Miall (2003) suggest that the time intervals longer than a second require a cognitive control since they are represented as discrete events rather than part of a predictable sequence, whereas repetitive movements lasting less than a second can be processed and controlled more automatically, through time mechanisms within the motor system itself (Lewis and Miall, 2003).

Our data extend this view suggesting that, for repetitive movements of less than one second, the amount by which a timing mechanism is activated - more cognitive, or event-based, and more automatic, or emergent - is correlated with the efficiency of the subject to be in time.

Chapter 7: Experiment VI

Kinesio taping improves the Timing Consistency in Subjects with Spino-Cerebellar Ataxia: Preliminary Data

7.1 Abstract

The cerebellum is a strongly implicated structure in the processes of timing and numerous studies have shown how cerebellar lesions determine an augmented variability in tasks of motor and perceptual timing. It was shown that individuals with cerebellar lesions are impaired in the production of sequences of discontinuous movements requiring event-based strategy. Conversely this population did not show impairment of rhythmic motor performance when continuous movements, requiring emergent timing, are executed. It was shown that KT tends to bias toward the emergent timing control for the production of rhytmic movements (Experiments III and V). Here we want to investigate whether KT, by changing the the timing process employed for the production of movements, is able to improve the timing consistency of IWFEs on patients with spino-cerebellar ataxia. We studied two time interval conditions (800 and 550 ms). Preliminary results show that KT, by modulating the timing processes, improves greatly the timing consistency of IWFEs. This is particularly evident for the condition in which IWFEs with 800 ms time interval are performed.

7.2 Introduction

Spino-cerebellar ataxia (SCA) is an autosomal dominant form of hereditary ataxia, appertaining to a group of hereditary ataxias, which include autosomal recessive forms as well, such as Friedrich's ataxia types and X -linked. The prevalence is estimated between 0.8 and 3.5: 100.000. SCA can be classified according to the function of the mutated gene, the affected chromosomal locus, or the genetic inheritance pattern; the various forms of SCA are characterized by typical signs: SCA1 and SCA3 show pyramidal signs such as hyperreflexia and spasticity; SCA2 can include parkinsonism or motor neuron diseases such as Amyotrophic Lateral Sclerosis; SCA12 and SCA13 are characterized by cognitive deficits; SCA17 can manifest in association with chorea. The onset of the disease is mostly belated, generally between 30 and 50 years of age; its progression is variable and the life expectancy reaches about 10-15 years in the case of SCA1, SCA2, SCA3 and 7 or normal regarding SCA5 and 14 (Jayadev and Bird, 2013).

SCA is characterized by a progressive loss of coordination and balance, combined with a reduction of fine manual coordination, speech and eye movement; moreover patients might exhibit symptoms such as ophthalmoplegia, spasticity and rigidity, neuropathy, muscular hypertonia, sensory disturbances and retinitis pigmentosa (Jayadev and Bird, 2013).

The cerebellum is a strongly implicated structure in the processes of timing, numerous studies have shown how cerebellar lesions determine an augmented variability in tasks of motor timing, perceptual timing and explicit timing (Gooch et al., 2010; Harrington et al., 2004; Ivry and Keele, 1989; Malapani et al., 1998; Spencer et al., 2003). However, the effects of cerebellar lesions on perceptual timing are more varied, with the reported deficits being marginal (Harrington et al., 2004; see also Ivry and Spencer, 2004), nonselective (Casini and Ivry, 1999), or restricted to specific duration ranges (Nichelli et al., 1996).

We displayed in the Experiment III that KT, an elastic band of cotton, is able to increase timing consistency in young healthy subjects.

Also, we showed that the processes for timing consistency are influenced by the application of KT. Specifically, we observed that the application of KT tend to bias toward the emergent timing control for the production of rhytmic movements.

In "Disrupted Timing of Discontinuous But Not Continuous Movements by Cerebellar Lesions" on individuals with unilateral cerebellar lesions were asked to perform timed tapping, intermittent circle drawing, and continuous circle drawing tasks. Performances were impaired only when tasks were executed with the ipsilesional hand and involved movements theorized to require event-based (discontinuous movements) but not emergent timing (continuous). It was concluded that temporal properties of continuous movements are emergent and reflect the operation of other control parameters not associated with the cerebellum (Spencer et al., 2003).

Starting from the notion that the cerebellum functions as an internal timing device in the milliseconds range, we wanted to investigate whether the application of KT, by changing the timing process employed for the production of movements, is able to improve the timing consistency on subjects with SCA. To investigate it, we use a rhytmic motor task in which both event-based and emergent components of timing are involved.

7.3 Methods

Participants

To date, five adults with SCA were enrolled for this study. According to the laterality score from the Edinburgh Handedness Inventory (Oldfield, 1971) all participants were right handed (98.0±4.5).

For four of these participants, genetic testing confirmed a variant of spinocerebellar ataxia (SCA1: one participant; SCA2: three participants). For the remaining fifth participant, the etiology of their cerebellar degeneration was unknown. The ataxics were all evaluated with the International Cooperative Ataxia Rating Scale (ICARS, see: Trouillas et al., 1997). The mean score was 25.8±4.3 (Table 8), indicating a mild to moderate level of ataxic disorder.

Participants were naive to the purpose of the study and they knew nothing about the KT method. In addition, they were no musically trained, and all reported no auditory impairments. Experimental procedures conformed to the declaration of Helsinki and were approved by the local Ethics Committee (Comitato Etico Area Vasta Centro AOUCareggi, Florence, Italy). Written informed consent was obtained from all participants.

Set up

The experimental setup is largely that used in the Experiment V, so here will be summarized briefly.

Each participant was tested individually, sitting upright on a chair with the feet on leg rest, wearing headphones (to reduce environmental noise and to deliver audio information; K 240 Studio, AKG Acoustics GmbH, Wien, AT). The participant's dominant forearm was placed on armrest, in a relaxed horizontal position. The wrist and hand of the participant were free to move in mid-air with no direct opposition, thus minimizing tactile information.

Differently to healthy subjects, the participants were asked to wear special glasses able to eliminate the lower part of the visual field. This strategy as well as the request to watch a point at eye level during the performance allowed to the subject to execute the movements without to observe the hand.

A triaxial accelerometer (ADXL330, Analog Devices Inc., Norwood, MA, USA) was placed on the dorsal aspect of hand, over the proximal part of the 2nd–3rd metacarpal bones. Sensor output was acquired and digitized at 200 Hz through PCI-6071E (12-Bit E Series Multifunction DAQ, National Instruments, Austin, TX, USA).

Streams of 16 clicks were produced using the audio editor Audacity (GNU/GPL, http://audacity.sourceforge.net/), via the function Generate Click. The audio files were constructed as a series of 20 ms sounds, set to white noise, followed by 530 ms of silence for the IOI of 550 ms or by 780 ms of silence for IOI of 800 ms.

For the KT (Kinesio® Tex Gold™ FP-2″ Red) application the participant, already seated on the chair with forearm in full pronation and rested on the armrest, was asked to keep the wrist in full flexion. KT was applied with a light length tension of 50% (Kase et al., 2003). The tensions of KT were assessed according to the method described in Kase (2003). KT was applied in all participants by the same investigator (Pelosin et al., 2013). KT was applied, according to a protocol previously reported in the experiment III.

Differently to healthy subjects, in this experiment each participant was taped employing the same technique as in the Kinesio Taping, but with non elastic 5 cm wide medical tape (Mefix; SHAM-KT).

Data format

Data Format is that used in all Experiments described previously.

Preliminary tests

A few days before starting the first session of the test, the subjects had a preliminary session in which they were tested in order to assess fine coordination, strength, as well as maximum movement speed of both dominant and non-dominant hands. Additionally, their auditory working memory was tested. The carried out tests are the nine hole peg test, the hand grip test, the maximum movement speed test, and the n-back test.

Nine Hole Peg Test. This test permits to evaluate fine coordination of both dominant and non-dominant hand. The setup was formed by a rectangular pegboard with nine holes, arranged in three rows by three, distant 3.2 centimeters from one another and 1.3 centimeters deep. A container, placed laterally, containing nine pegs of wood, had a diameter of 0.64 cm and 3.2 cm long (Rolyan 9-Hole Peg Test Kit - Model A8515). The pegboard was placed in front of the subject, with the peg container on the side of the tested hand. The test consisted of taking a peg at a time from the container, and inserting it in the furthest hole from the tested hand, gradually filling all the holes; once this task was done, the subject had to remove all the pegs from the holes always one at a time starting from last peg that has been inserted and terminating with the first peg that has been placed inside the hole (Mathiowetz et al., 1985). The duration of the test was measured by a stopwatch, started when the subject touched the first peg, and stopped when the last peg removed from the keyhole was placed inside the container (Mathiowetz et al., 1985). Before executing the actual test, a few practice trials were performed with both hands. The dominant hand was tested first.

Handgrip Force Test. This test was performed to evaluate the strength of the subjects' hand. To carry out the test we used a portable digital dynamometer (Baseline 12-0286 Electronic Smedly Hand Dynamometer, 200 lbs Capacity) able to measure the force exerted by the subject. The test was done individually for each hand in a sitting position: the subject had to tighten his/her grip on the dynamometer with one hand, and apply the pressure for 5 seconds. The process was repeated four times for each hand for a total of eight repetitions. Before the actual session, a few practice trials were performed in order to clarify the task to the subjects.

Maximum Movement Speed Test. A rapid movement task was included to ensure that the base intervals in the time reproduction task did not exceed subjects' maximum movement rate. Cerebellar patients performed IWFEs at the maximum movement speed with dominant and not dominant hands. The mean movement rate across five trials (10 s each) measured their maximum movement speed (Harrington et al., 2004).

N-back Test. We used a slightly varied version of the N-back test. N-back is a test used to evaluate the Auditory Working Memory (AWM). Using a special software, different sounds were played to the subject, and each time he/she heard a sound which is identical to the previous one played, he had to click the mouse. Our testing differs from the traditional one since we used sounds instead of letters. The peculiarity of this test is the possibility to examine AWM in various levels, by changing the so-called N, namely, the frequency of identical following sounds that indicates to click the mouse. We used two types of N-back test: the N-back test 1, where the task given to the subject was to click the mouse when the sound heard was identical to the previous one, and the N-back 2,where the target sound is played two sounds before the current one (Monk et al., 2011; Stoodley et al., 2012).

Finally, this part was terminated with the execution of neurological tests.

The ICARS (Schmitz-Hübsch et al., 2006) was performed to quantify the severity of the tested subjects' ataxia, while the Inventory of Non-Ataxia Signs (INAS) was performed to evaluate the presence of non-ataxic signs (Jacobi et al., 2013). ICARS represents a clinical evaluation scale of certain parameters that are characteristic of ataxic disorders. These disorders are caused by lesions of the cerebellum or its afferent connections; and may be accompanied by some neurological symptoms. ICARS is one of the three rating scales of ataxic disorders, together with the Friedreich Ataxia Rating Scale (FARS) and the Scale for the Assessment and Rating of Ataxia (SARA).

Among these, ICARS, published in 1997 (Trouillas et al., 1997), was the first standardized clinical evaluation scale of ataxic disorders (Schmitz-Hübsch et al., 2006). ICARS features four sub-scores regarding respectively, posture and balance (item 1-7, score 0-34), limb coordination (item 8-14, score 0-52), speech (item 15-16, score 0-8) and oculomotor functions (item 17-19, score 0-6, Schmitz-Hübsch et al., 2006). The purpose of the compartmentalization was to provide separate values of the different components of the ataxic disorder (Schmitz-Hübsch et al., 2006). Each subject, who underwent ICARS, gained a score based on the results obtained in each item. The scale itself ranges from a minimum of 0 to a maximum of 100, represented by the maximum value of ataxia reached on this scale (Schmitz-Hübsch et al., 2006).

Session

Each subject had participated in three sessions, one with no KT (N-KT), one with Kinesio taping (KT), and one with SHAM-KT, which were performed at least at a three days' distance. The KT and SHAM-KT session started approximately 10 minutes after mounting the tape since this interval is needed to overcome perception of tape on the skin (Kase et al., 2013). The order of the three sessions was randomized between participants.

In the reproduction task, the metronome produced 16 beats and then turned off. Participants entrained to the metronome, attempting to complete a cycle coincident with the beat of the metronome (i.e., maintaining an in-phase 1:1 relationship between repeated wrist's flexion-extensions and the tempo of the audio; paced phase). When the metronome turned off the participants attempted to produce movements with the same time interval for approximately one minute (unpaced phase).

In each session IWFEs sets were performed with dominant and non-dominant hand, before with one and later with the other hand. A total of 24 sets of IWFEs were performed in each session, whose 12 sets with each hand. Six sets were performed unimanually at each of two interval durations - 550 and 800 ms - conditions. The order of hands with which to perform IWFEs and interval duration was randomized (Fig. 30). The KT sessions started 10 min after mounting the tape to overcome perception of tape on the skin (Kase et al., 2013). At end of each KT session participants removed the KT.

Only the data from the unpaced phase were analysed. The first two IWFEs of the continuation phase were discarded and the analyses were performed on the remaining IWFEs (Harrington et al., 2004)

7.4 Results

7.4.1 Dominant Hand

The accuracy was calculated before the CVs of IWFEs, for both 800 and 550 ms conditions. On average, participants were equally proficient at reproducing the required interval durations for both conditions, in N-KT, KT, and SHAM-KT cases (Fig 31A, B).

The CV of IWFEs durations was used to investigate whether the KT influences the timing variability (precision) of IWFEs performances for both 800 and 550 ms conditions. Δ% of CVs was calculated to measure percentage differences of CVs between cases in which KT and SHAM-KT was applied, and the N-KT case (see Experiment IV for the computation of Δ%).

In the 800 ms condition, values CVs are remarkably different between N-KT (6.16%), and KT or the SHAM-KT cases (4.4% and 5.69%, respectively; Fig. 32A) with an improvement of precision of IWFEs by ≈ 19% with KT application and by ≈ 7%. with SHAM-KT (Fig. 32B). Also in the 550 ms condition, values of CVs are different between N-KT (4.79%) and the other KT cases (4.47% and 5.14%, respectively; Fig. 32C), but while KT is able to improve the temporal precision (≈ 6%), SHAM-KT augments the timing variability of IWFEs (≈ -7%; Fig. 32D).

The computation of series of (windowed) lag-one autocorrelations, herein abbreviated $w\gamma(1)$, for each set of IWFEs, produced allowed to explore whether KT might influence timing control processes (see Experiment II, III, and V). Δ%

of wγ(1) was calculated to measure percentage differences between cases in which KT and SHAM-KT was applied, and the N-KT case.

In the 800 ms condition, the mean wγ(1) was positive for N-KT (0.15±0.15), remarkably positive for KT (0.23±0.14), and slighty positive for SHAM-KT (0.09±0.15; Fig. 33A); the employment of the emergent timing component with KT was augmented by 52%, while it was reduced by using SHAM-KT (- 39%; Fig. 33B). In the 550 ms condition, wγ(1) values were strikingly positive in all cases (N-KT = 0.22±0.13; KT = 0.23±0.16; SHAM-KT = 0.19±0.16; Fig. 33C) and they were higher than those obtained for IOI of 800 ms. Wγ(1) was not influenced by KT (4%) and slighty modified by SHAM-KT as shown from Δ% (- 14%; Fig. 33D).

7.4.2 Non-dominant Hand

As for hand dominant, the accuracy was calculated before the CVs of IWFEs, for both 800 and 550 ms conditions. On average, participants were equally acurated to reproduce the required interval durations for both conditions, in N-KT, KT, and SHAM-KT cases (Fig 34A, B).

In the 800 ms condition, values CVs are different between N-KT and KT (5.82% and 5.36%, respectively), while insignificantly different between N-KT and SHAM-KT (5.82% and 5.85%, respectively; 35A). KT improves the timing precision of IWFEs by ≈ 8% (Fig. 35B). In the 550 ms condition, while CVs of N-KT and SHAM-KT are almost equal (5.64% and 5.67%, respectively), CVs of N-KT and KT are different (5.64% and 5.22%, respectively, Fig. 35C). KT improved the timing precision of IWFEs by ≈ 8% (Fig. 35D).

Interestingly, it is to mention that mean CVs of the 800 and 550 ms conditions in N-KT cases are nearly equal. This means that the ratio of the standard deviation divided by the timed interval - or CV - is not constant across the two different duration intervals. One main finding from several time perception and production studies is that timing variability in the hundreds of millisecond to second range increases constantly as a function of the interval to be timed, in accordance to Weber's law (Karampela et al., 2015). KT, by reducing the CV value in the 550 ms condition, recreates the physiological constant ratio across the two different intervals (Fig. 36).

Windowed Lag-one Autocorrelation

In the 800 ms condition, the mean wγ(1) was positive for N-KT, KT and SHAM-KT (0.16±0.14; 0.12±0.12; 0.12±0.14, respectively; Fig. 37A). The employment of the emergent timing component was reduced when KT and KT-SHAM were applied (≈ - 28% and - 27%, respectively; Fig. 37B). In the 550 ms condition, wγ(1) values were positive in all cases (N-KT = 0.13±0.15; KT = KTT-MF = 0.16±0.17; SHAM-KT = 0.13±0.16; Fig. 37C). The employment of the emergent timing component was augmented by KT (≈19%). The modulation the emergent timing component by SHAM-KT was irrelevant (- 3%; Fig. 37D).

Interestingly, it is to mention that mean wγ(1) of the 800 and 550 ms conditions in N-KT cases are nearly equal, with mean wγ(1) value of the 800 ms higher than that of 550 ms. It has been shown that, in healthy subjects, as the frequency of movement increases, the movement resembles an oscillation and the processing can be equated with emergent timing (Repp, 2008b; 2011b; Bravi et al., 2015). KT recreates in the cerebellar subjects the phisiological trend observed in healthy subjects, on the one hand by reducing the mean wγ(1) of 800 ms time interval and on the other hand augmenting the mean wγ(1) of the 550 ms time interval (Fig. 38).

7.5 Opening conclusion

In general, preliminary results show that KT, by modulating the timing processes, improves greatly the timing consistency of IWFEs. This is particularly evident for the condition in which IWFEs with 800 ms time interval are performed.

However, given the small sample of subjects and the lack of control group we refrain from discussing the data in our possession.

Future Investigations and General Conclusion

Future investigations on direct brain–behavior relationship between motor performance changes due to Kinesio taping application and neural activity could to extend and clarify previous results obtained.

Also, to investigate how changes in motor performance during the recall of simple and complex auditory stimuli are related to a particular pattern of neural activity could allow advancing our knowledge about on how perception may influence action (Zatorre et al., 2007). In addition, how specific musical sequences are encoded and stored in the brain is a neglected area of research, and little information is present in literature on the impact of listen/perception of unfamiliar music on self-paced oscillatory movements (Leaver et al., 2009). To compare neural/motor behavioral responses to familiar and unfamiliar music could give basic information that in the program of neurorehabilitation, where rhythmic auditory stimulation is used as method to regain gait deficits could be taken in account (Ashoori et al., 2015).

For what concerns timing mechanisms and the relationship between them during a rhythmic performance, our data confirm the mutual exclusive model: we demonstrate that subjects can exploit either the event-based or the emergent timing mode, or the two mode in alternation, but in all cases each mode appears to be exclusive.

In addition we show that timing mechanisms can be modulated by environmental stimuli. Audio stimuli, and in particular metronome, elicits event-based timing while Kinesio taping elicits emergent timing. Finally, Janzen and colleagues have shown that movement-based expertise is associated with enhanced timing, but these effects depend on the nature of the training: athletes performed significantly better than musicians and controls in the circle-drawing task (an emergent timing task), whereas musicians were more precise in the finger tapping task (an event-based timing task).

Expertise was found to influence the timing strategy adopted to maintain precise rhythmic movements, suggesting that event and emergent timing mechanisms are not strictly tied to specific tasks, but can both be adopted to achieve precise timing (Baer et al., 2013; Janzen et al., 2014).

By using a rhytmic motor task, in which both event-based and emergent timing component are elicited, we show that the amount by which a timing mechanism is activated - more cognitive, or event-based, and more automatic, or emergent - is correlated with the efficiency of the subject to be in time.

Finally, on the basis of promising results obtained by Kinesio taping in increasing sensorimotor synchronization in healthy subjects, future research could be done to test the effectiveness of Kinesio taping on some motor disorders like the musician's dystonia, a task-specific focal dystonia, which is manifested as a painless muscular incoordination, loss of voluntary motor control of refined movements, and alteration of timing parameters (Altenmüller and Jabusch, 2009). In the last years the musician's dystonia has been re-discussed as a sensorimotor disorder, leading to the scrutiny of proprioceptive rehabilitation strategies to reduce involuntary muscle activity (Avanzino et al., 2014). KT could be one of these strategies.

Abbreviations

AWM = Auditory Working Memory

bpm = beats per minute

Cl = while listening to a stream of clicks

Cl2 = after 2 minutes from the end of the Cl condition

Cl5 = after 5 minutes from the end of the Cl condition

CV = coefficients of variation

FARS = Friedreich Ataxia Rating Scale

FDI = Filled Duration Illusion

fKT = facilitatory KT application with light tension

fKT-T = facilitatory KT application with moderate tension

Fr = free, in absence of auditory information

ICARS = International Cooperative Ataxia Rating Scale

iKT = inhibitory KT application with light tension

IOI = Interonset Interval

ISI = inter-stimulus interval

INAS = Inventory of Non-Ataxia Signs

IWFEs = isochronous wrist's flexion-extensions

KT = Kinesio® Tex taping

MEG = magnetoencephalography

Mu = while listening to an excerpt of music

Mu2 = after 2 minutes from the end of the Mu condition

Mu5 = after 5 minutes from the end of the Mu condition

N-KT = no KT

SARA = the Scale for the Assessment and Rating of Ataxia

SCA = Spino-cerebellar ataxia

Figures and Captions

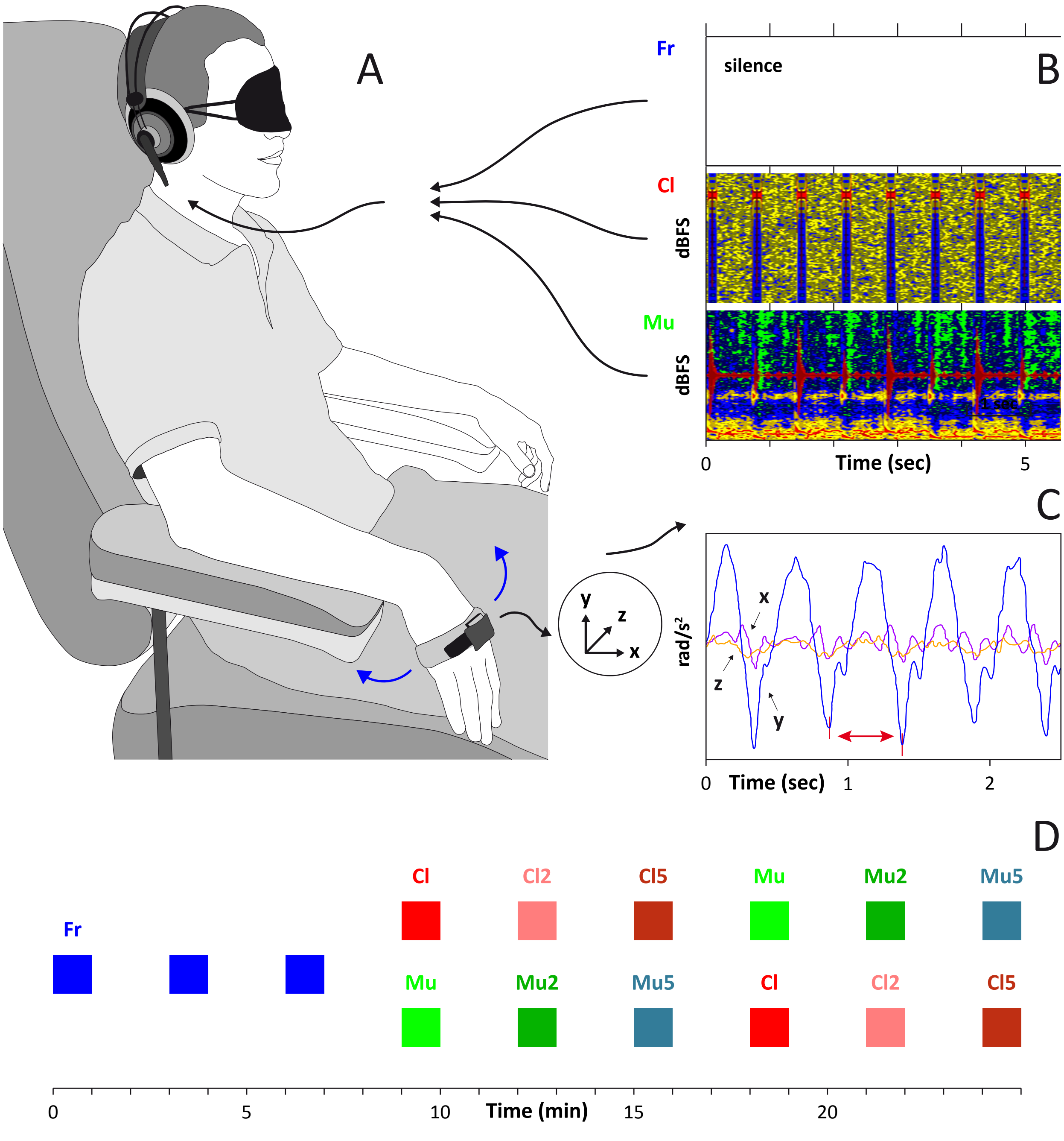

A
B
C
D
Fr
silence
Cl
dBFS
Mu
dBFS
0
Time (sec)
5
y
z
x
rad/s²
x
z
y
0
Time (sec)
1
2
Cl
Cl2
Cl5
Mu
Mu2
Mu5
Fr
Mu
Mu2
Mu5
Cl
Cl2
Cl5
0
5
10
Time (min)
15
20

Figure 1

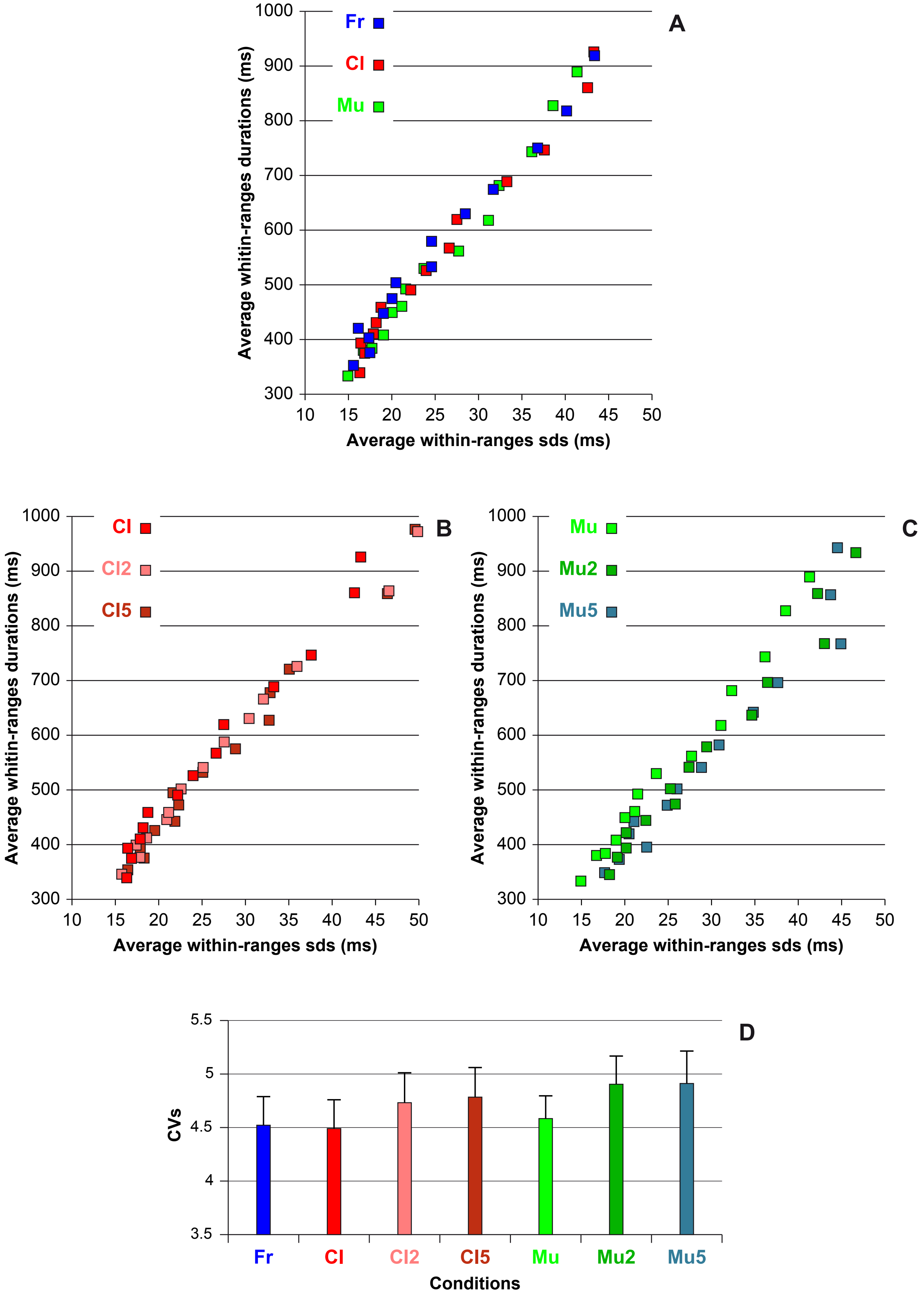

A
Fr
Cl
Mu
Average whitin-ranges durations (ms)
300
400
500
600
700
800
900
1000
Average within-ranges sds (ms)
10
15
20
25
30
35
40
45
50
B
Cl
Cl2
Cl5
Average whitin-ranges durations (ms)
Average within-ranges sds (ms)
C
Mu
Mu2
Mu5
Average within-ranges durations (ms)
Average within-ranges sds (ms)
D
CVs
3.5
4
4.5
5
5.5
Fr
Cl
Cl2
Cl5
Mu
Mu2
Mu5
Conditions

Figure 2

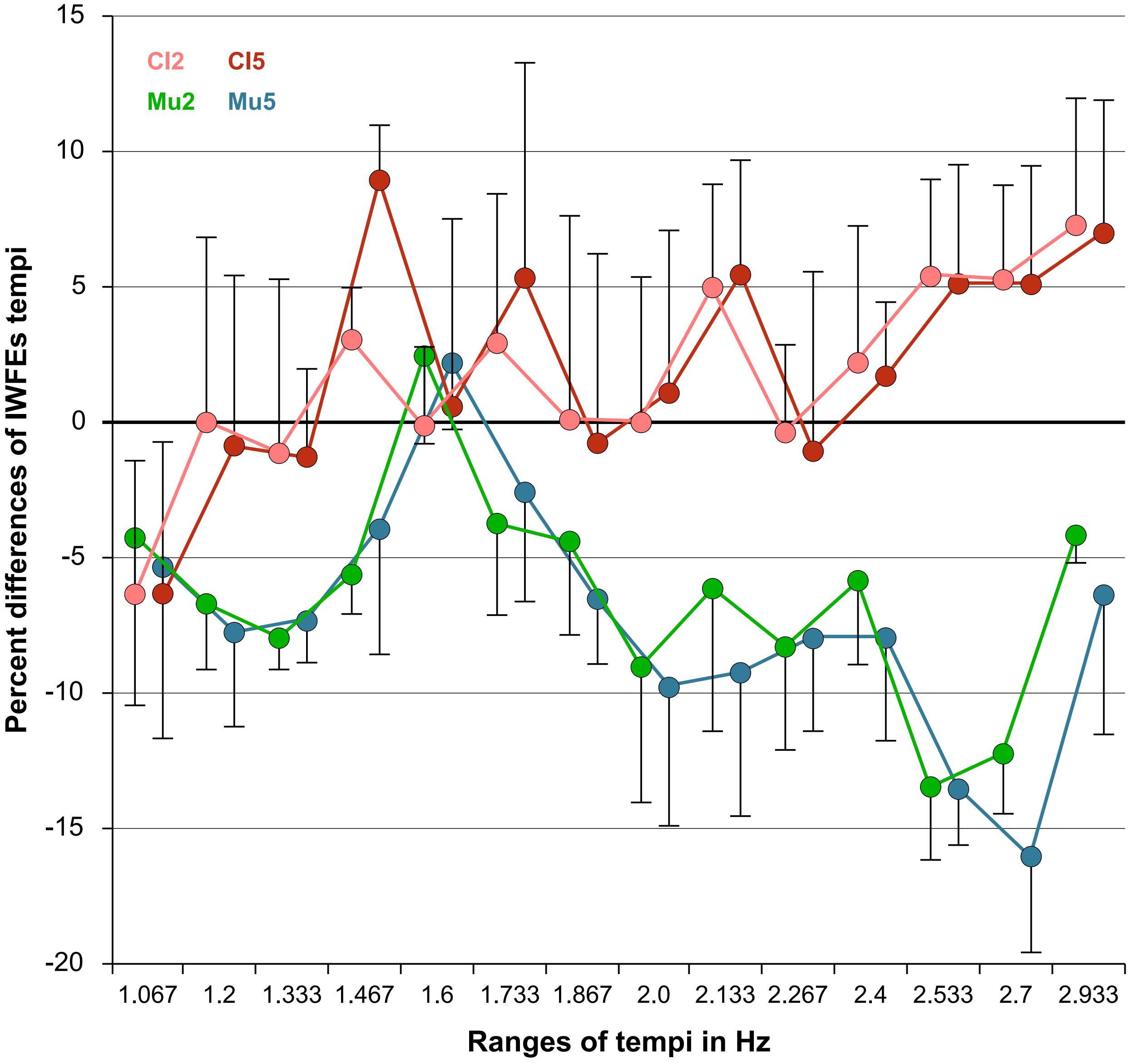

Cl2
Cl5
Mu2
Mu5
Percent differences of IWFEs tempi
15
10
5
0
-5
-10
-15
-20
1.067
1.2
1.333
1.467
1.6
1.733
1.867
2.0
2.133
2.267
2.4
2.533
2.7
2.933
Ranges of tempi in Hz

Figure 3

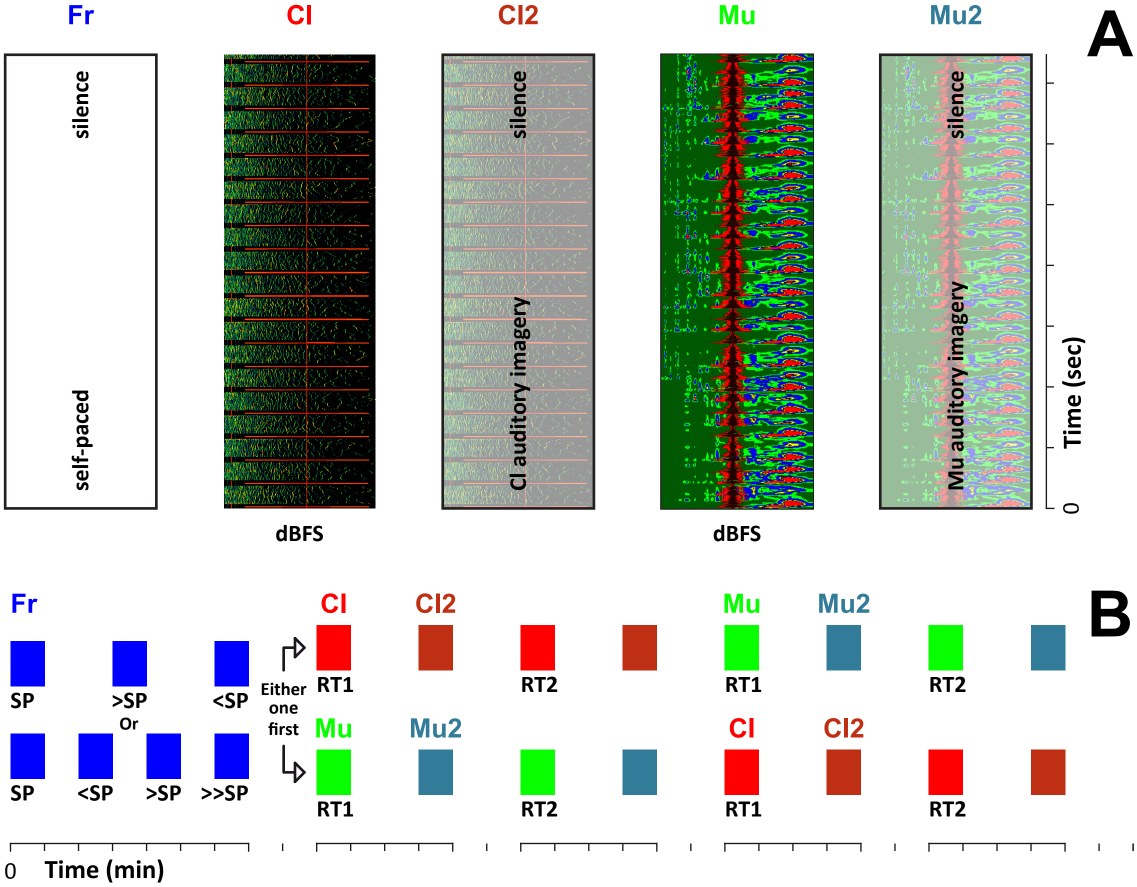

Fr
Cl
Cl2
Mu
Mu2
A
silence
self-paced
Cl auditory imagery
Mu auditory imagery
dBFS
dBFS
Time (sec)
0
B
Fr
SP
>SP
<SP
Or
SP
<SP
>SP
>>SP
Either one first
Cl
Cl2
Mu
Mu2
RT1
RT2
RT1
RT2
Mu
Mu2
Cl
Cl2
RT1
RT2
RT1
RT2
0
Time (min)

Figure 4

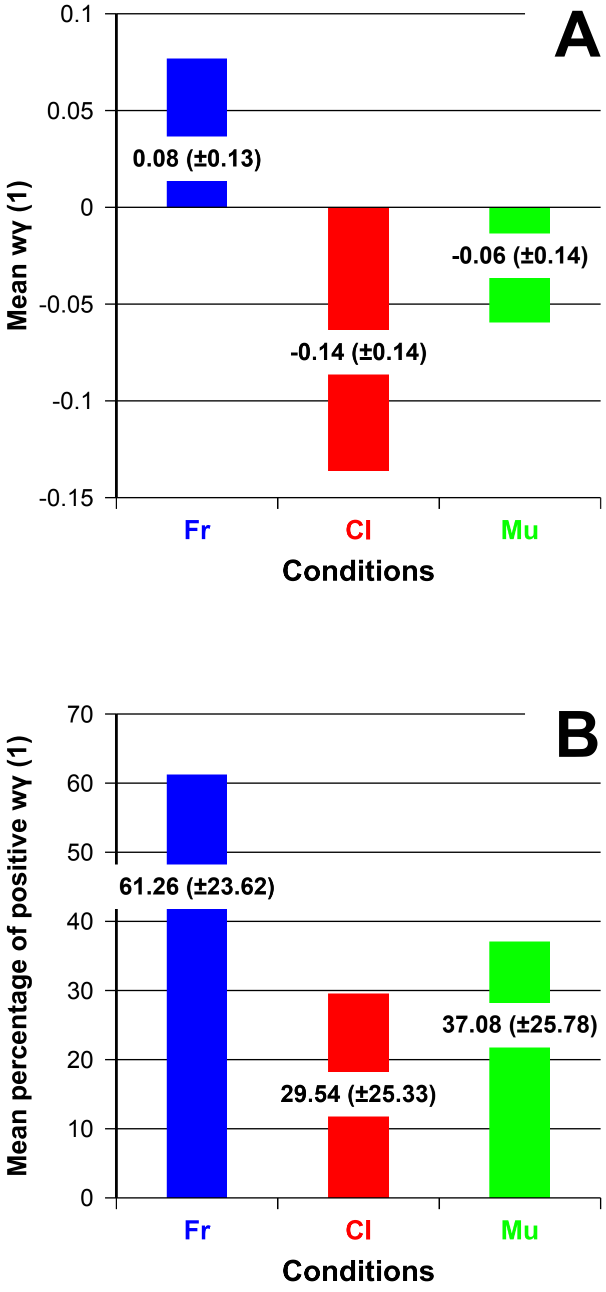

A
Mean wγ (1)
0.1
0.05
0
-0.05
-0.1
-0.15
0.08 (±0.13)
-0.14 (±0.14)
-0.06 (±0.14)
Fr
Cl
Mu
Conditions
B
Mean percentage of positive wγ (1)
70
60
50
40
30
20
10
0
61.26 (±23.62)
29.54 (±25.33)
37.08 (±25.78)
Fr
Cl
Mu
Conditions

Figure 5

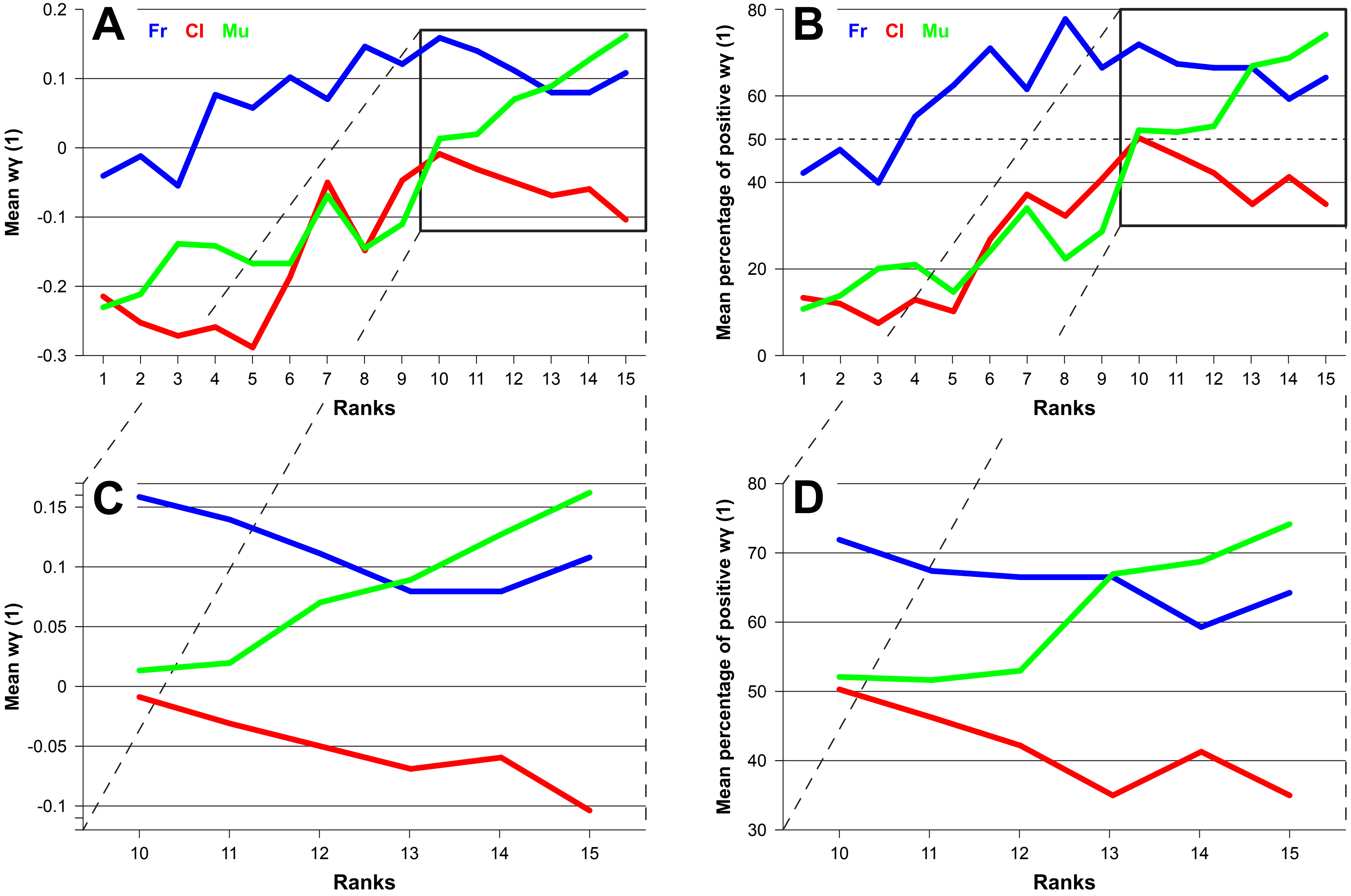

A
Fr
Cl
Mu
Mean wγ (1)
0.2
0.1
0
-0.1
-0.2
-0.3
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
Ranks
B
Fr
Cl
Mu
Mean percentage of positive wγ (1)
80
60
50
40
20
0
Ranks
C
Mean wγ (1)
0.15
0.1
0.05
0
-0.05
-0.1
10
11
12
13
14
15
Ranks
D
Mean percentage of positive wγ (1)
80
70
60
50
40
30
Ranks

Figure 6

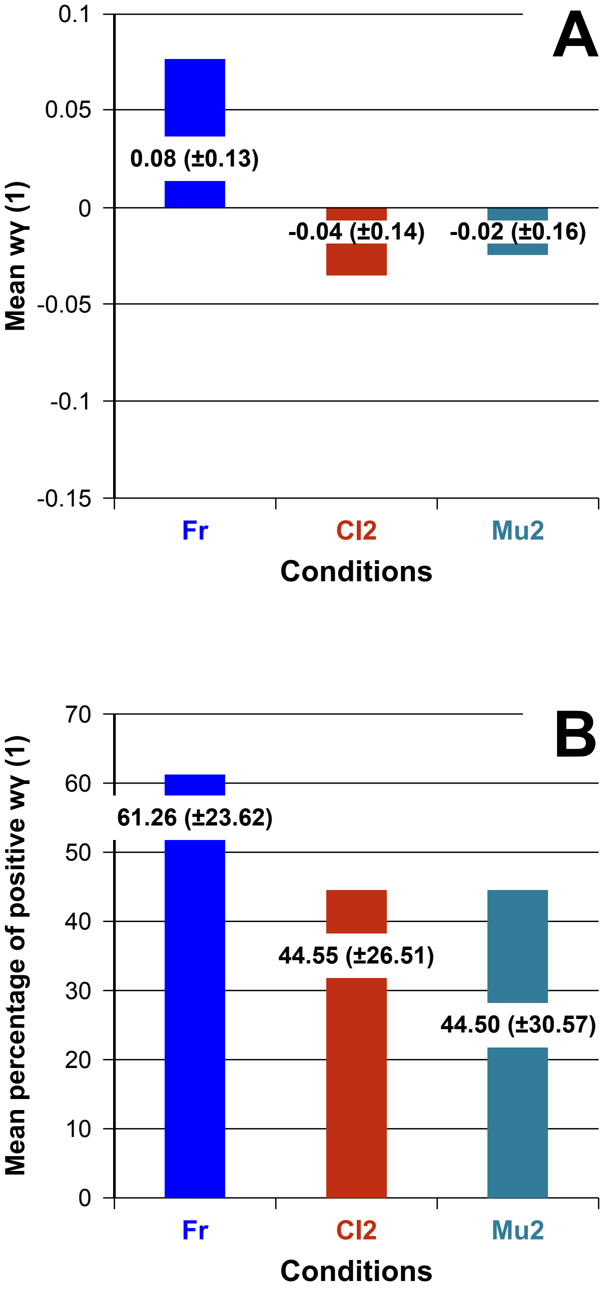
A
0.1
0.05
0
-0.05
-0.1
-0.15
Mean wγ (1)
0.08 (±0.13)
-0.04 (±0.14)
-0.02 (±0.16)
Fr
Cl2
Mu2
Conditions
B
70
60
50
40
30
20
10
0
Mean percentage of positive wγ (1)
61.26 (±23.62)
44.55 (±26.51)
44.50 (±30.57)
Fr
Cl2
Mu2
Conditions

Figure 7

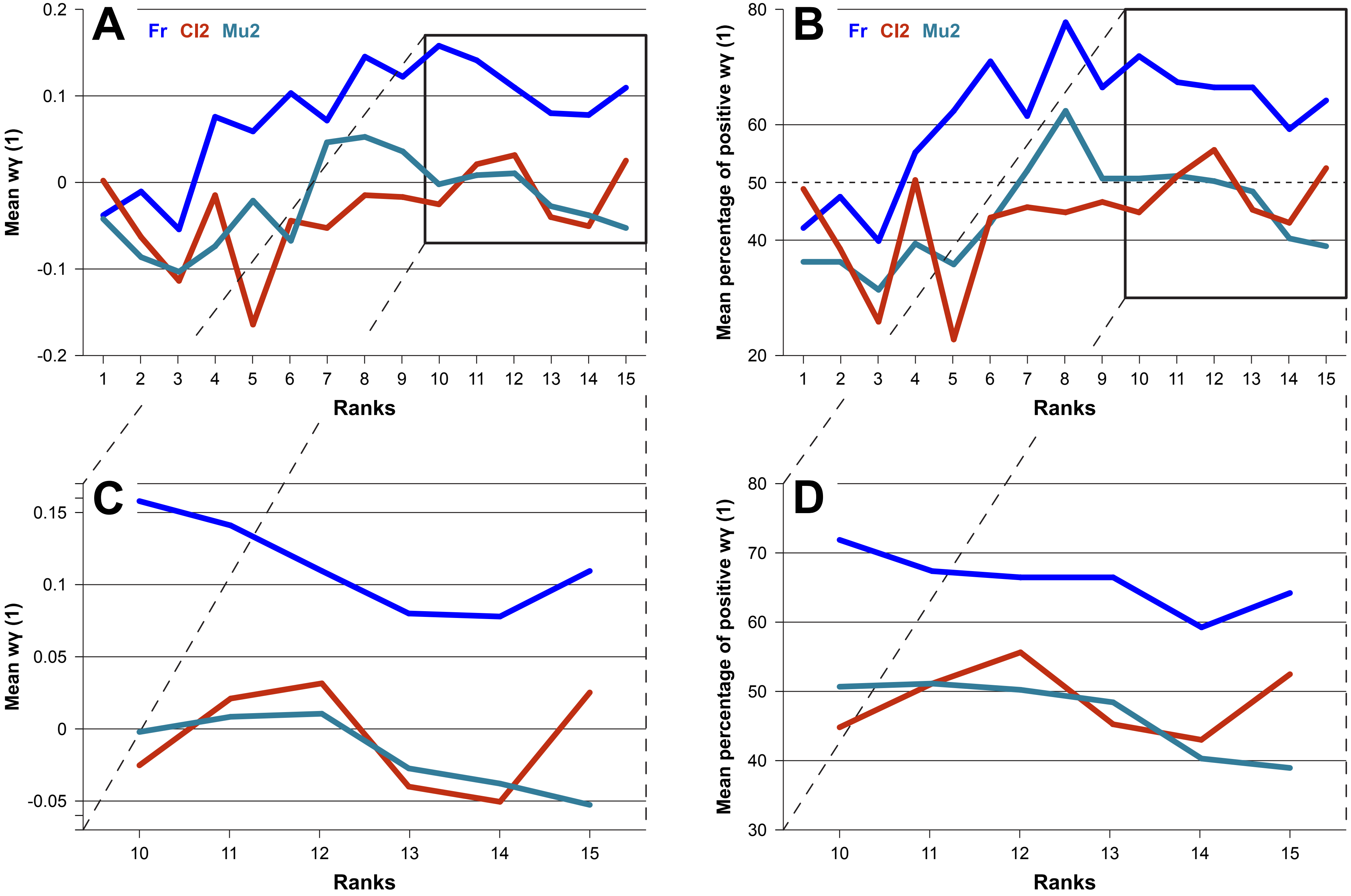

A
Fr
Cl2
Mu2
Mean wγ (1)
0.2
0.1
0
-0.1
-0.2
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
Ranks
B
Fr
Cl2
Mu2
Mean percentage of positive wγ (1)
80
60
50
40
20
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
Ranks
C
Mean wγ (1)
0.15
0.1
0.05
0
-0.05
10
11
12
13
14
15
Ranks
D
Mean percentage of positive wγ (1)
80
70
60
50
40
30
10
11
12
13
14
15
Ranks

Figure 8

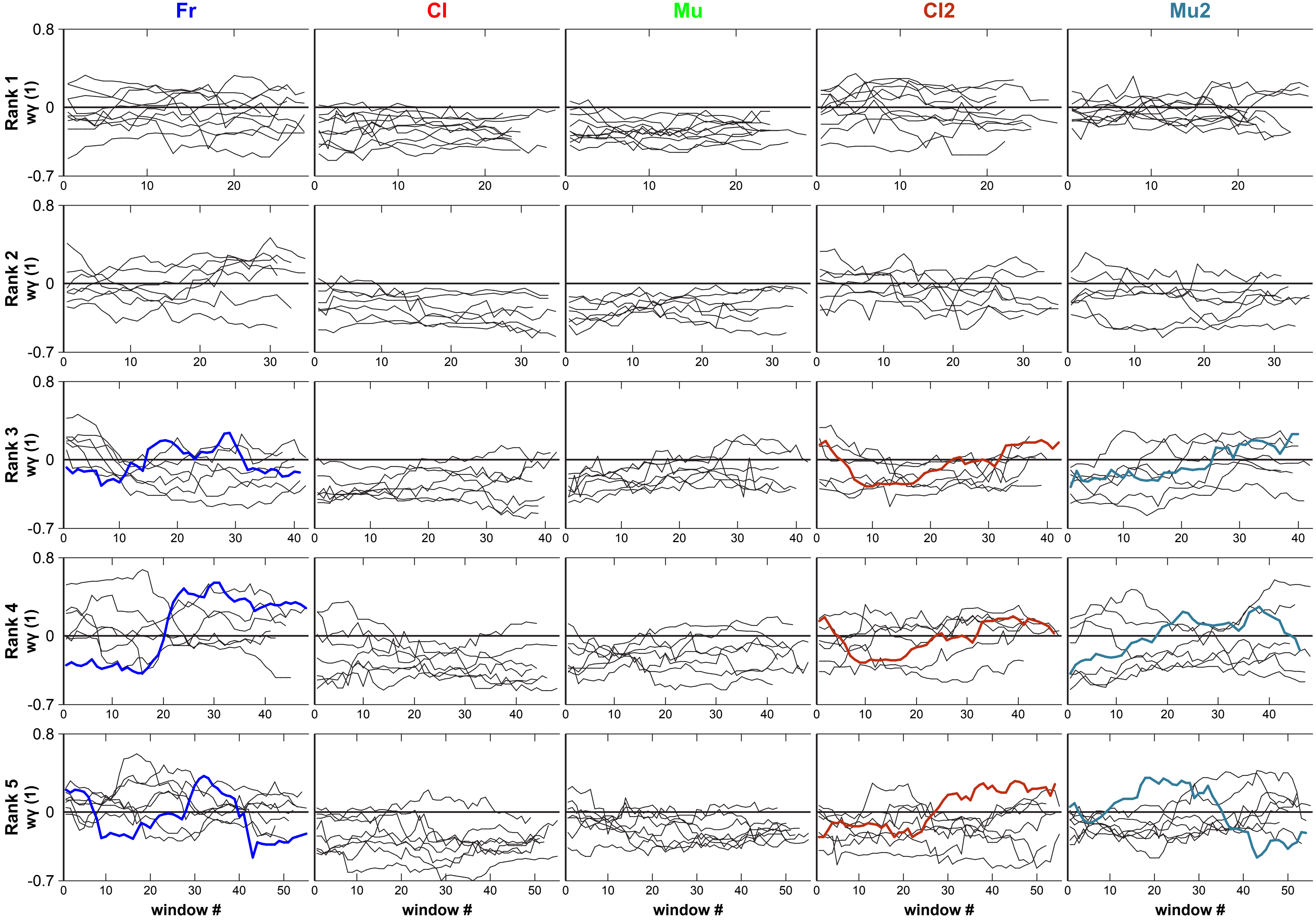

Fr
Cl
Mu
Cl2
Mu2
Rank 1
Rank 2
Rank 3
Rank 4
Rank 5
wγ (1)
0.8
0
-0.7
0
10
20
30
40
50
window #

Figure 9

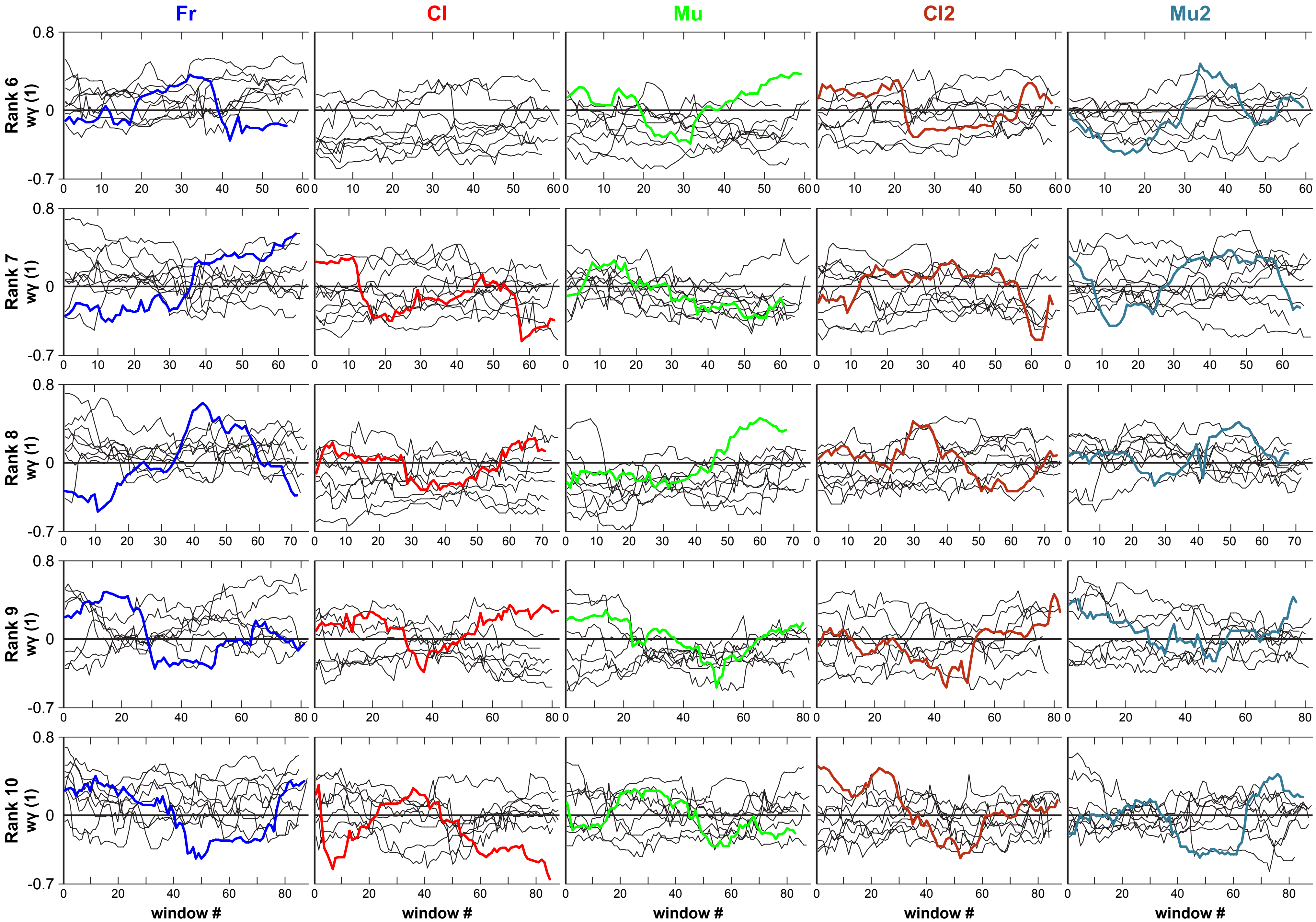

Fr
Cl
Mu
Cl2
Mu2
Rank 6
Rank 7
Rank 8
Rank 9
Rank 10
wγ (1)
0.8
0
-0.7
0
10
20
30
40
50
60
70
80
window #

Figure 10

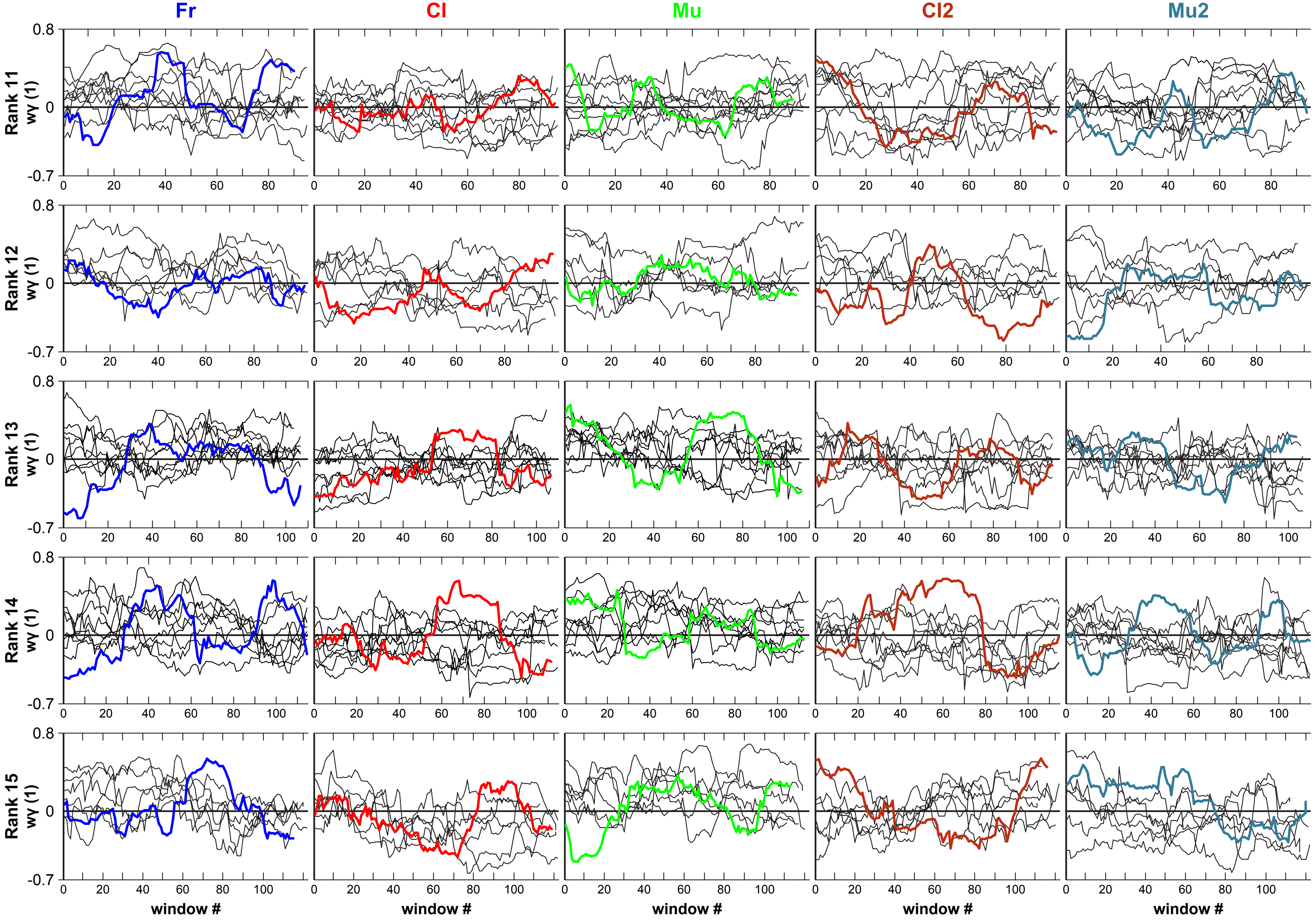

Fr
Cl
Mu
Cl2
Mu2
Rank 11
Rank 12
Rank 13
Rank 14
Rank 15
wγ (1)
0.8
0
-0.7
0
20
40
60
80
100
window #

Figure 11

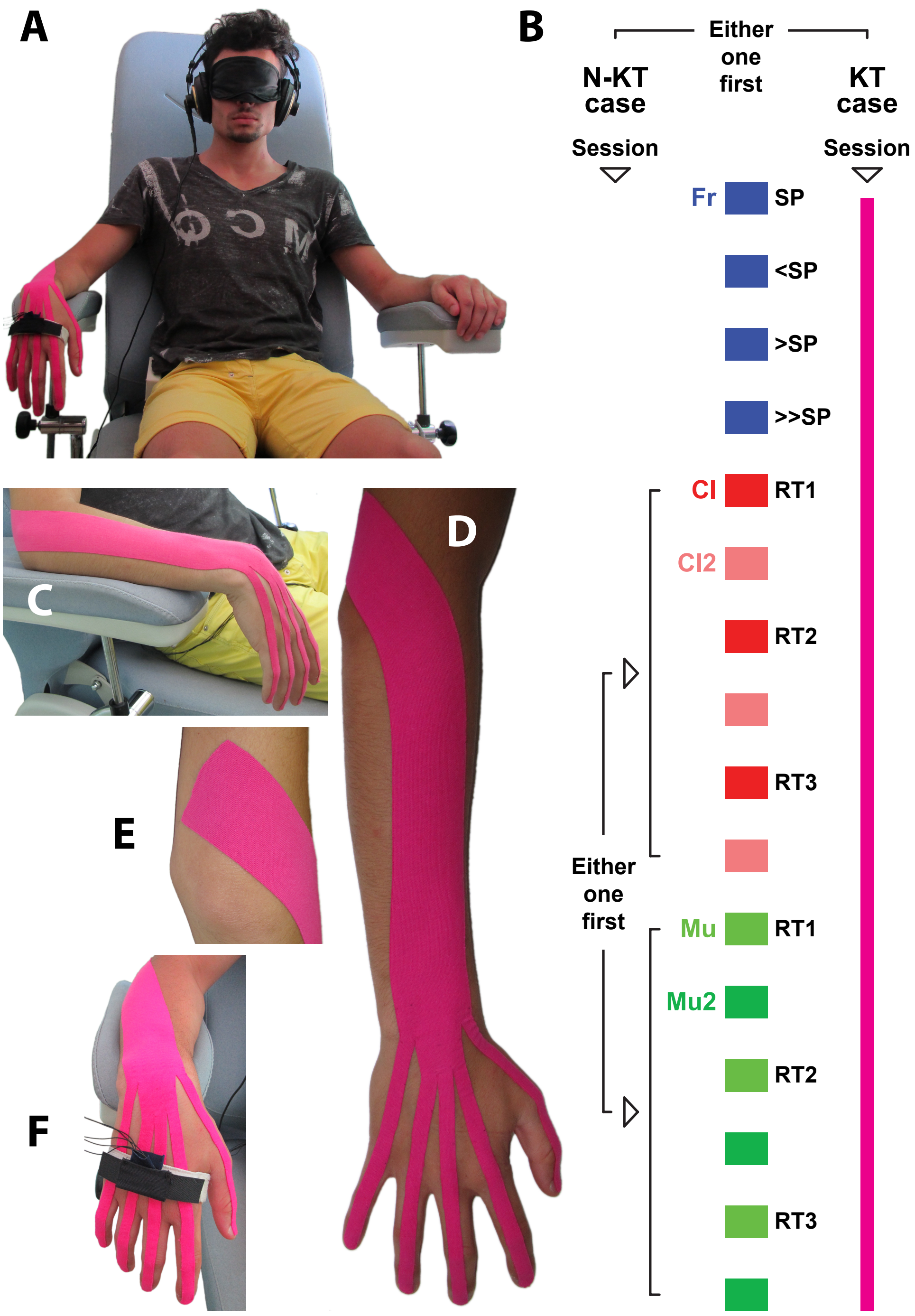

A
B
Either
one
first
N-KT
case
KT
case
Session
Session
Fr
SP
<SP
>SP
>>SP
Cl
RT1
Cl2
RT2
RT3
Either
one
first
Mu
RT1
Mu2
RT2
RT3
C
D
E
F

Figure 12

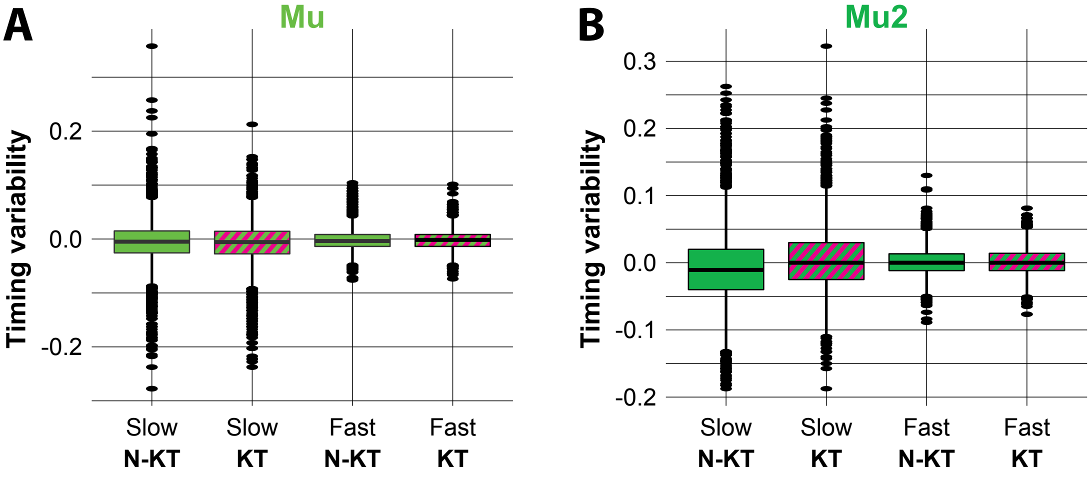

A
Mu
Timing variability
0.2
0.0
-0.2
Slow
N-KT
Slow
KT
Fast
N-KT
Fast
KT
B
Mu2
Timing variability
0.3
0.2
0.1
0.0
-0.1
-0.2
Slow
N-KT
Slow
KT
Fast
N-KT
Fast
KT

Figure 13

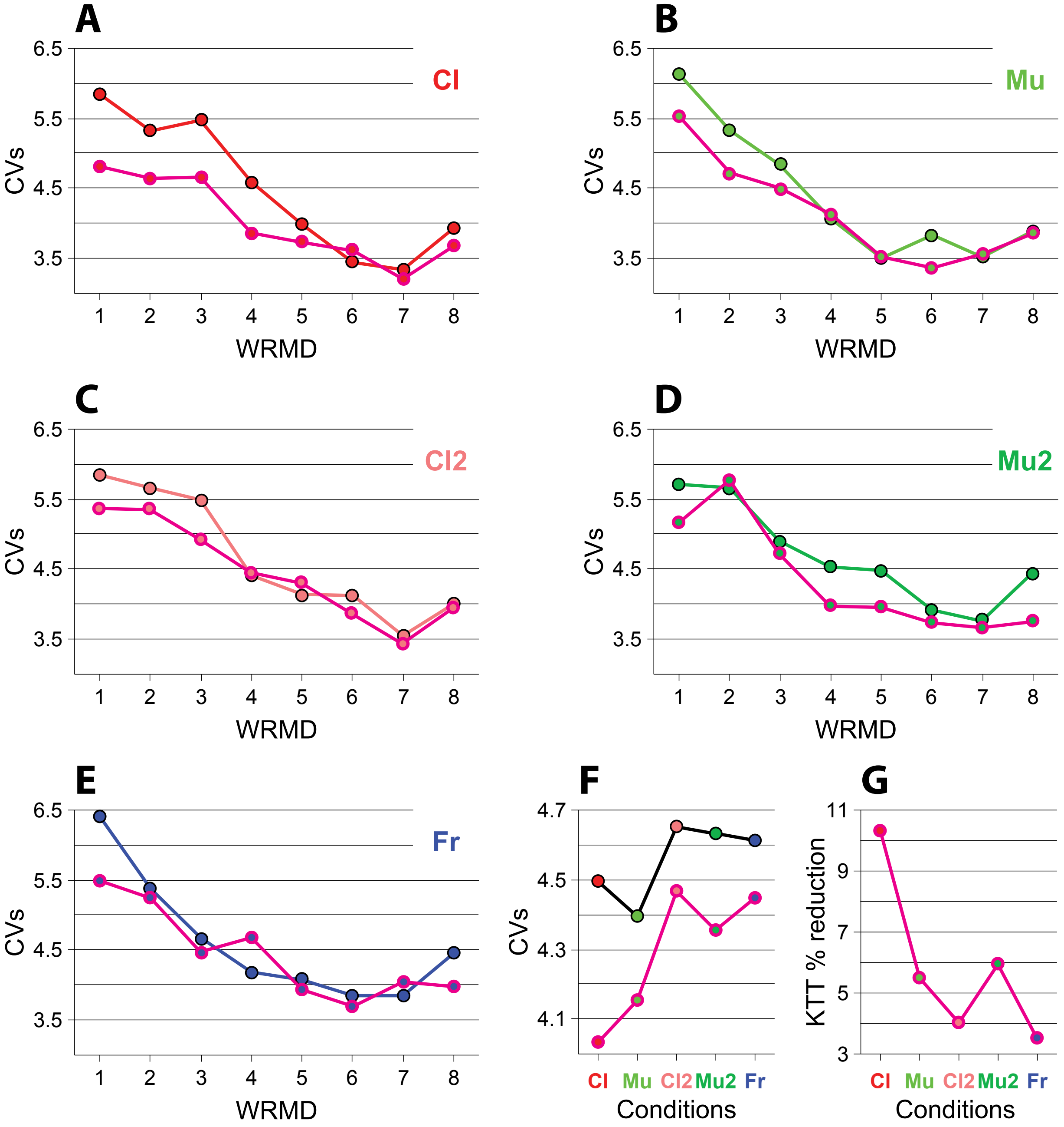

A
6.5
5.5
4.5
3.5
CVs
Cl
1 2 3 4 5 6 7 8
WRMD
B
Mu
C
Cl2
D
Mu2
E
Fr
F
4.7
4.5
4.3
4.1
Cl Mu Cl2 Mu2 Fr
Conditions
G
11
9
7
5
3
KTT % reduction

Figure 14

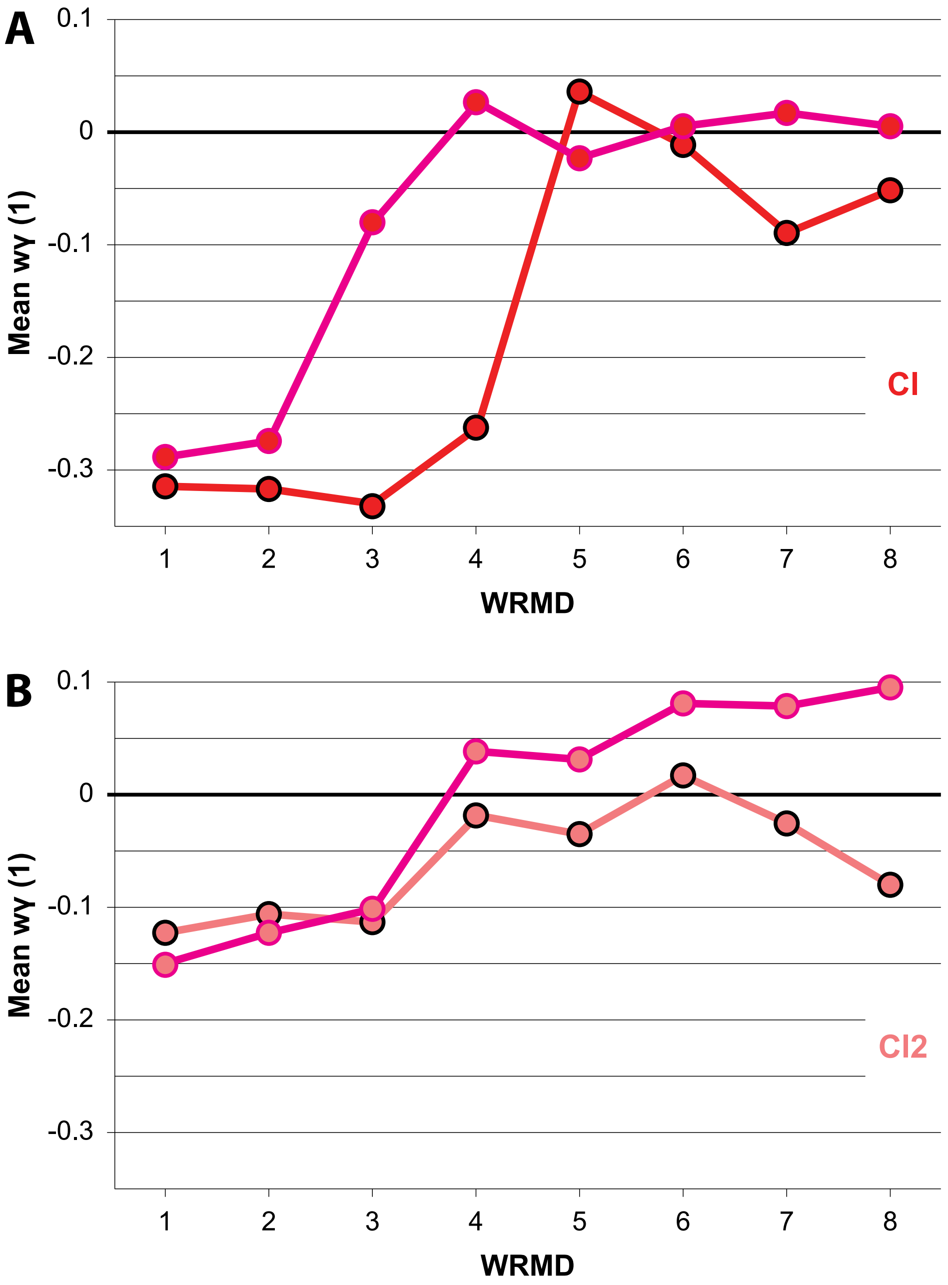
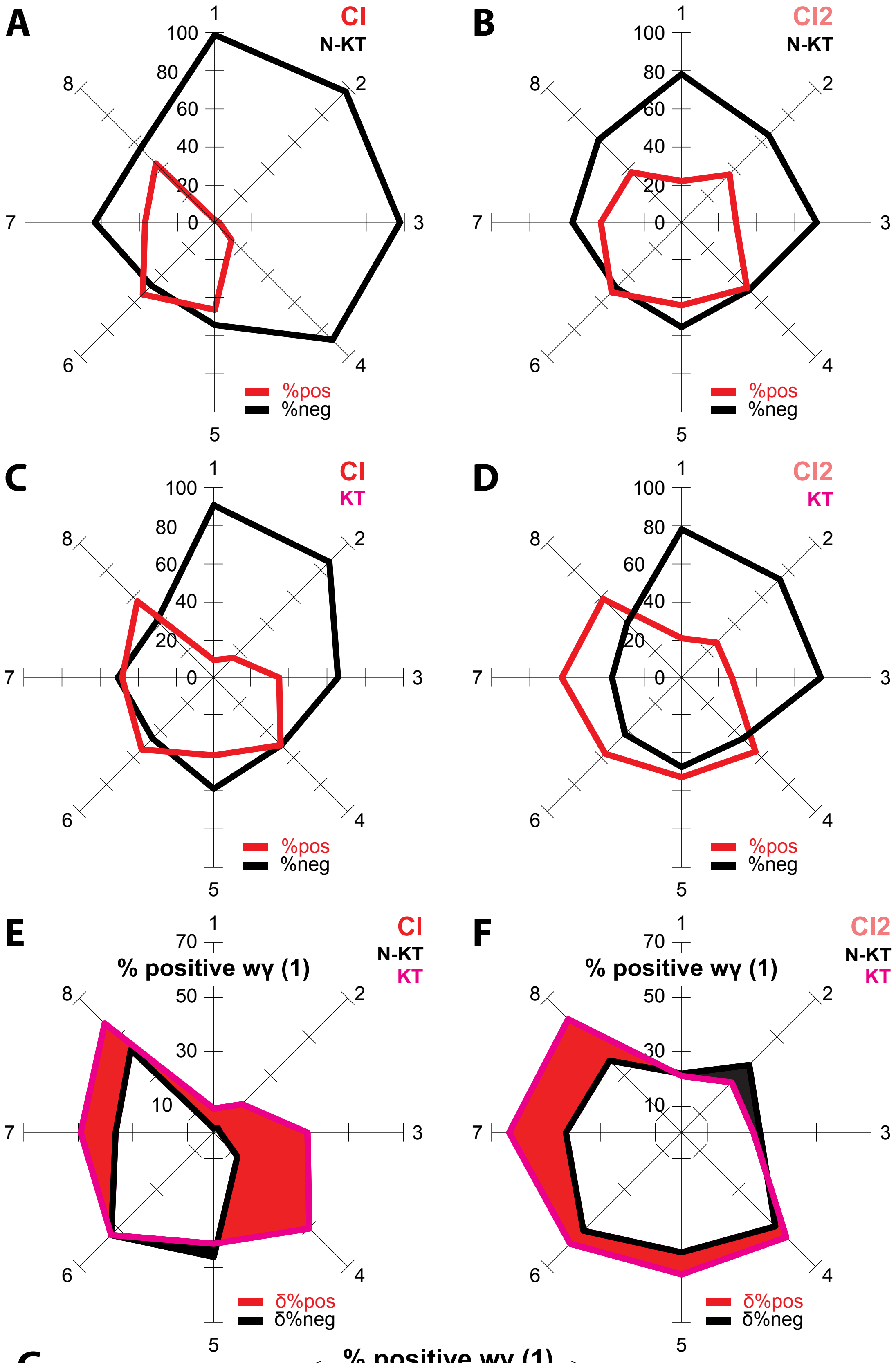

A
0.1
0
-0.1
-0.2
-0.3
Mean wγ (1)
1
2
3
4
5
6
7
8
WRMD
CI
B
0.1
0
-0.1
-0.2
-0.3
Mean wγ (1)
1
2
3
4
5
6
7
8
WRMD
CI2

Figure 15



G

% positive wγ (1)

CI

N-KT	KT	KT δ%pos
24.73	38.57	55.96

CI2

N-KT	KT	KT δ%pos
38.91	45.26	16.30

Figure 16

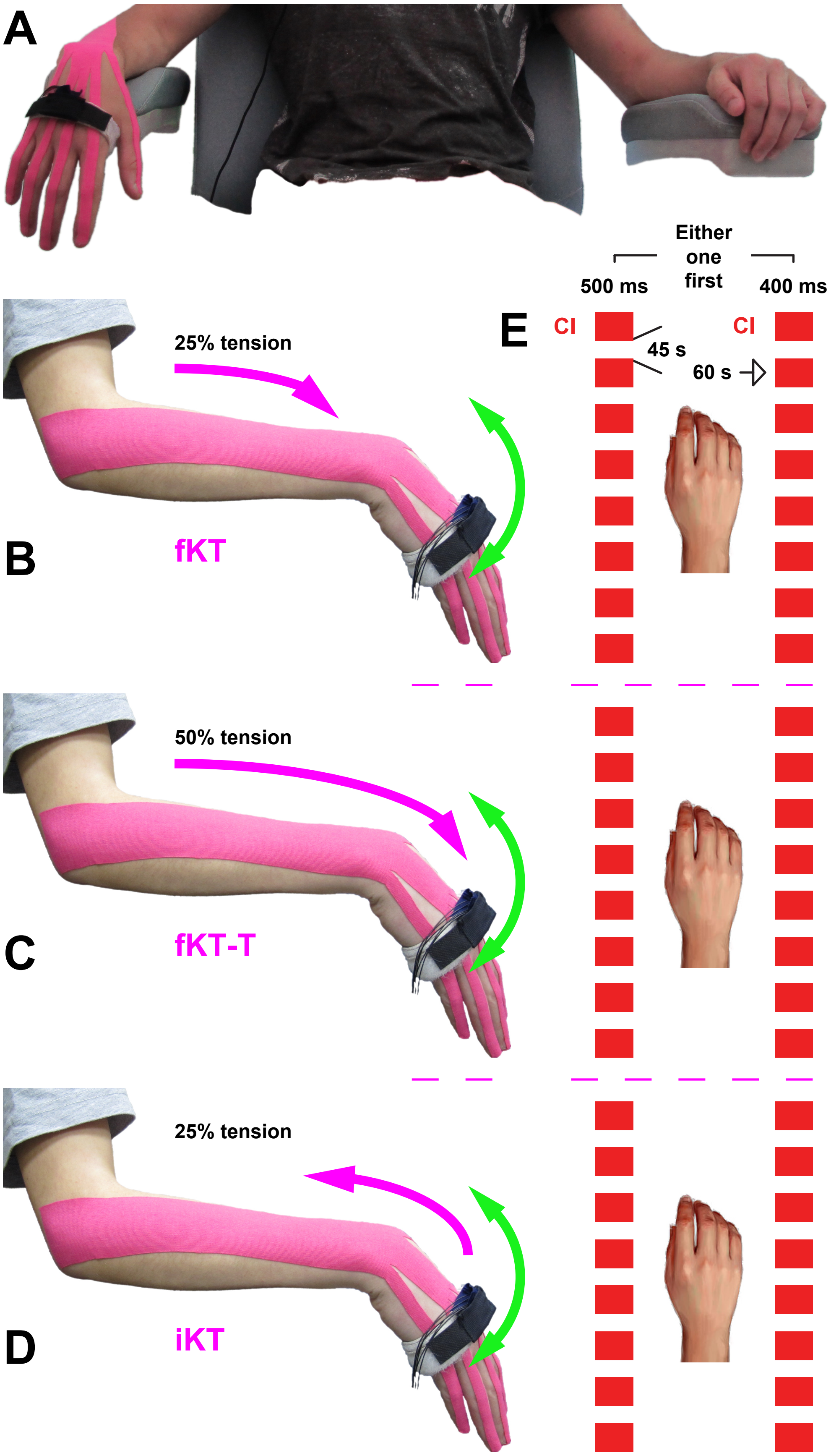

A
Either
one
first
500 ms
400 ms
E
CI
CI
45 s
60 s
25% tension
B
fKT
50% tension
C
fKT-T
25% tension
D
iKT

Figure 17

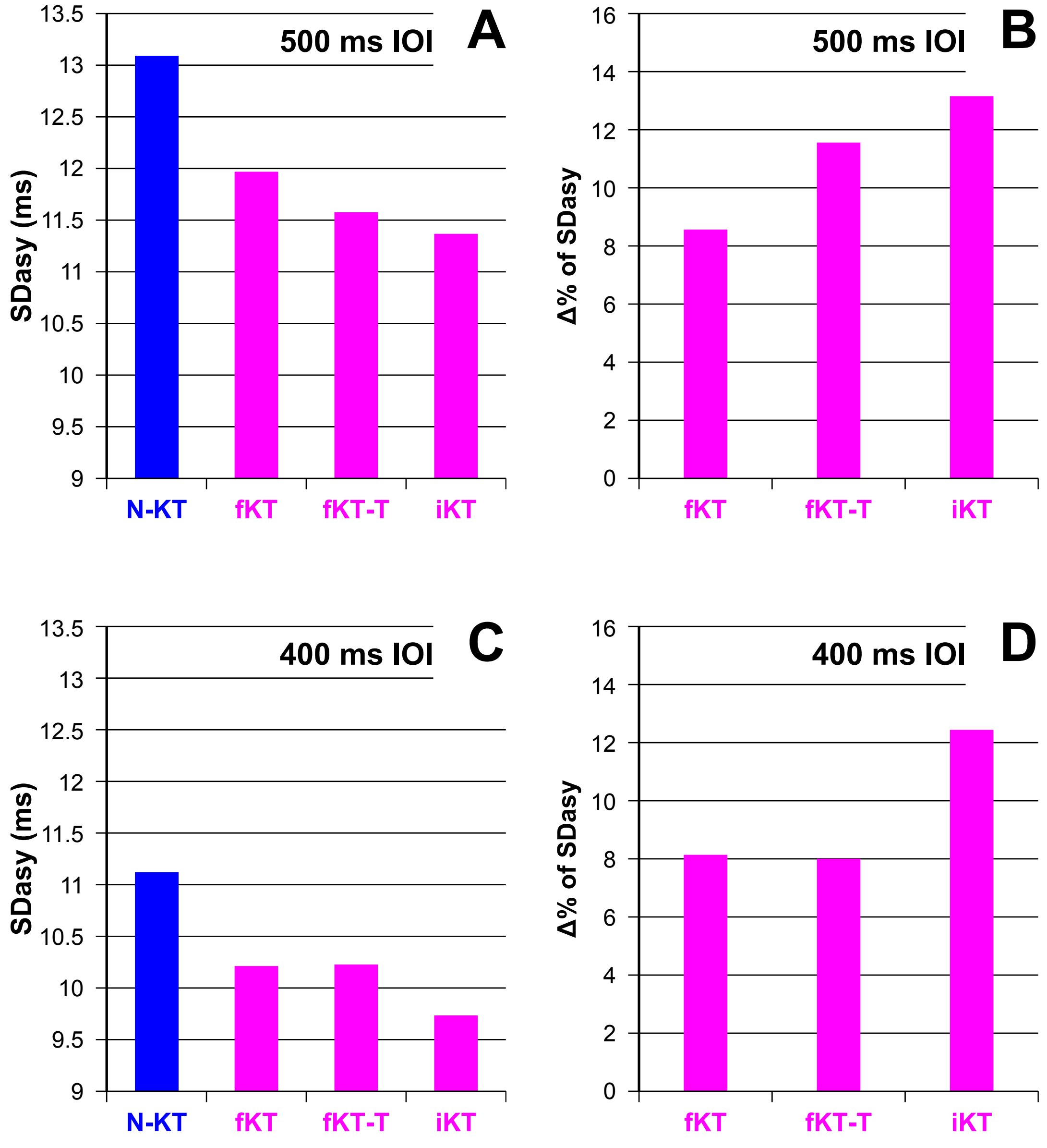

A
500 ms IOI
SDasy (ms)
13.5
13
12.5
12
11.5
11
10.5
10
9.5
9
N-KT
fKT
fKT-T
iKT
B
500 ms IOI
Δ% of SDasy
16
14
12
10
8
6
4
2
0
fKT
fKT-T
iKT
C
400 ms IOI
SDasy (ms)
13.5
13
12.5
12
11.5
11
10.5
10
9.5
9
N-KT
fKT
fKT-T
iKT
D
400 ms IOI
Δ% of SDasy
16
14
12
10
8
6
4
2
0
fKT
fKT-T
iKT

Figure 18

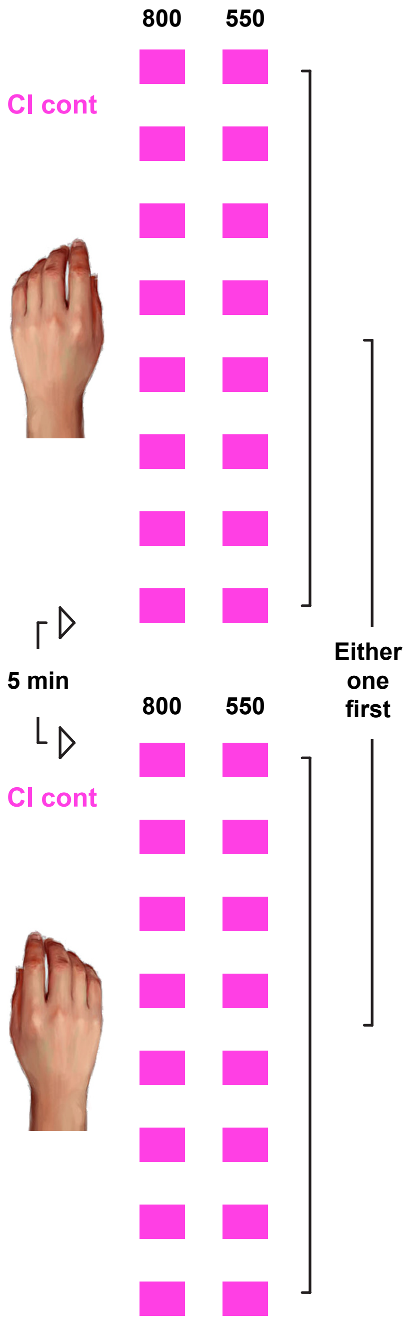


Figure 19

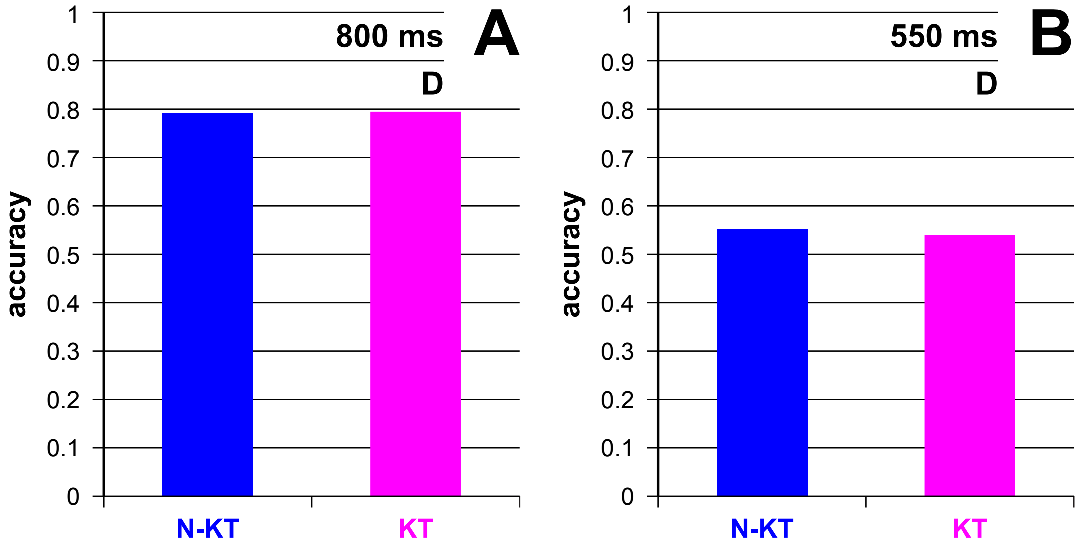


Figure 20

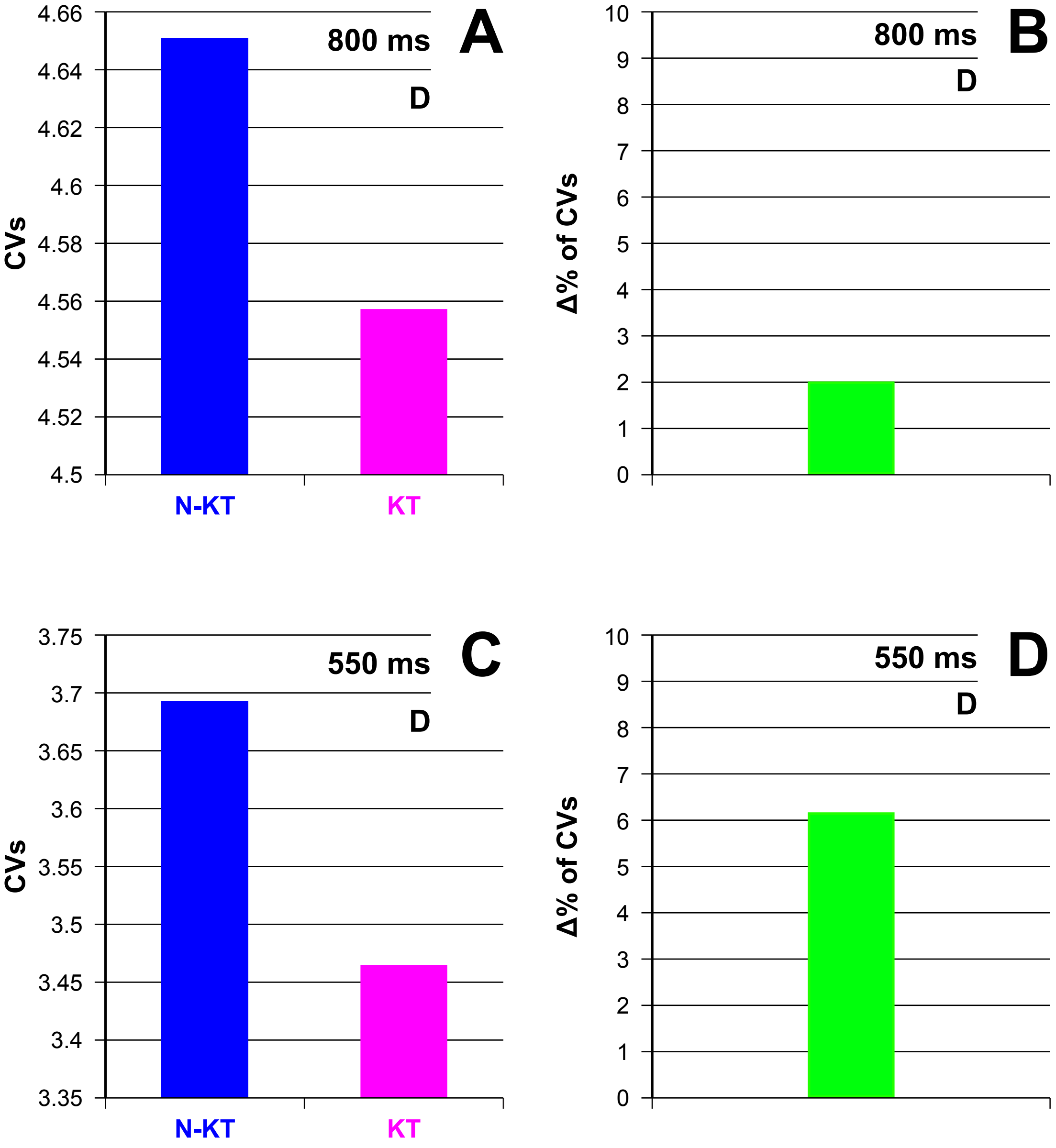

A
800 ms
D
CVs
4.66
4.64
4.62
4.6
4.58
4.56
4.54
4.52
4.5
N-KT
KT
B
800 ms
D
Δ% of CVs
10
9
8
7
6
5
4
3
2
1
0
C
550 ms
D
CVs
3.75
3.7
3.65
3.6
3.55
3.5
3.45
3.4
3.35
N-KT
KT
D
550 ms
D
Δ% of CVs
10
9
8
7
6
5
4
3
2
1
0

Figure 21

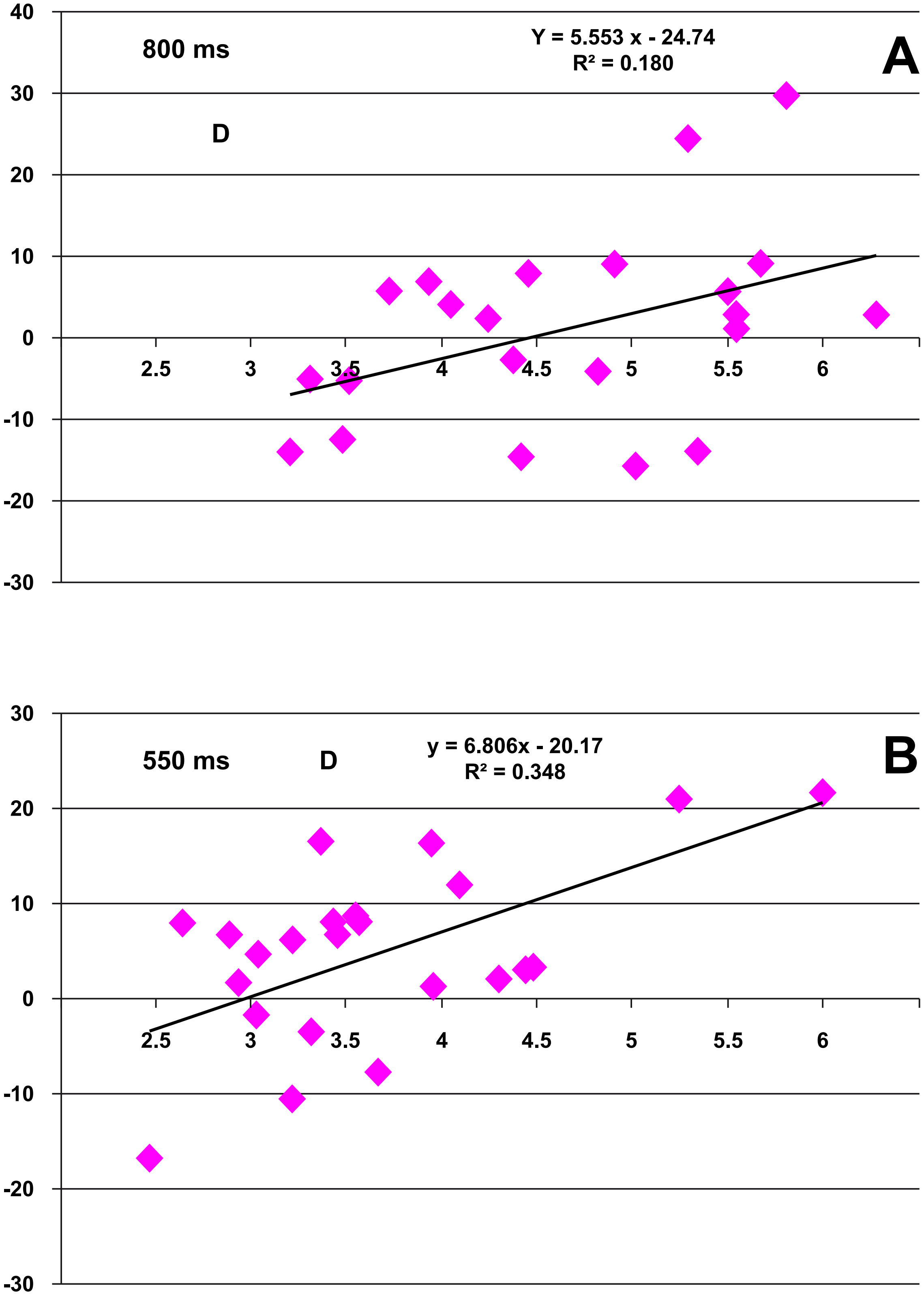

40
30
20
10
0
-10
-20
-30
800 ms
D
Y = 5.553 x - 24.74
R² = 0.180
A
2.5
3
3.5
4
4.5
5
5.5
6
30
20
10
0
-10
-20
-30
550 ms
D
y = 6.806x - 20.17
R² = 0.348
B
2.5
3
3.5
4
4.5
5
5.5
6

Figure 22

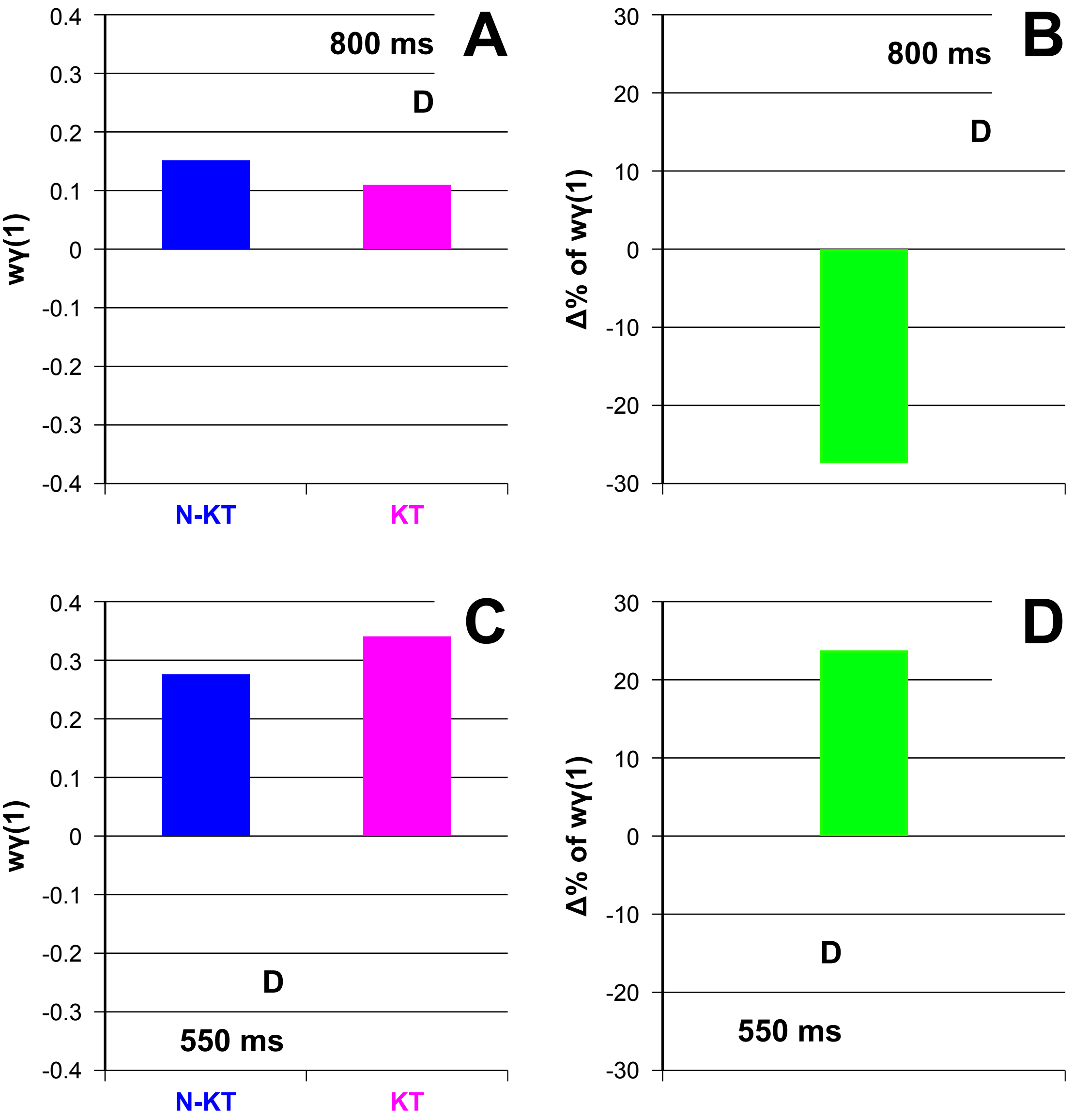

A
800 ms
D
wγ(1)
0.4
0.3
0.2
0.1
0
-0.1
-0.2
-0.3
-0.4
N-KT
KT
B
800 ms
D
Δ% of wγ(1)
30
20
10
0
-10
-20
-30
C
D
550 ms
wγ(1)
0.4
0.3
0.2
0.1
0
-0.1
-0.2
-0.3
-0.4
N-KT
KT
D
D
550 ms
Δ% of wγ(1)
30
20
10
0
-10
-20
-30

Figure 23

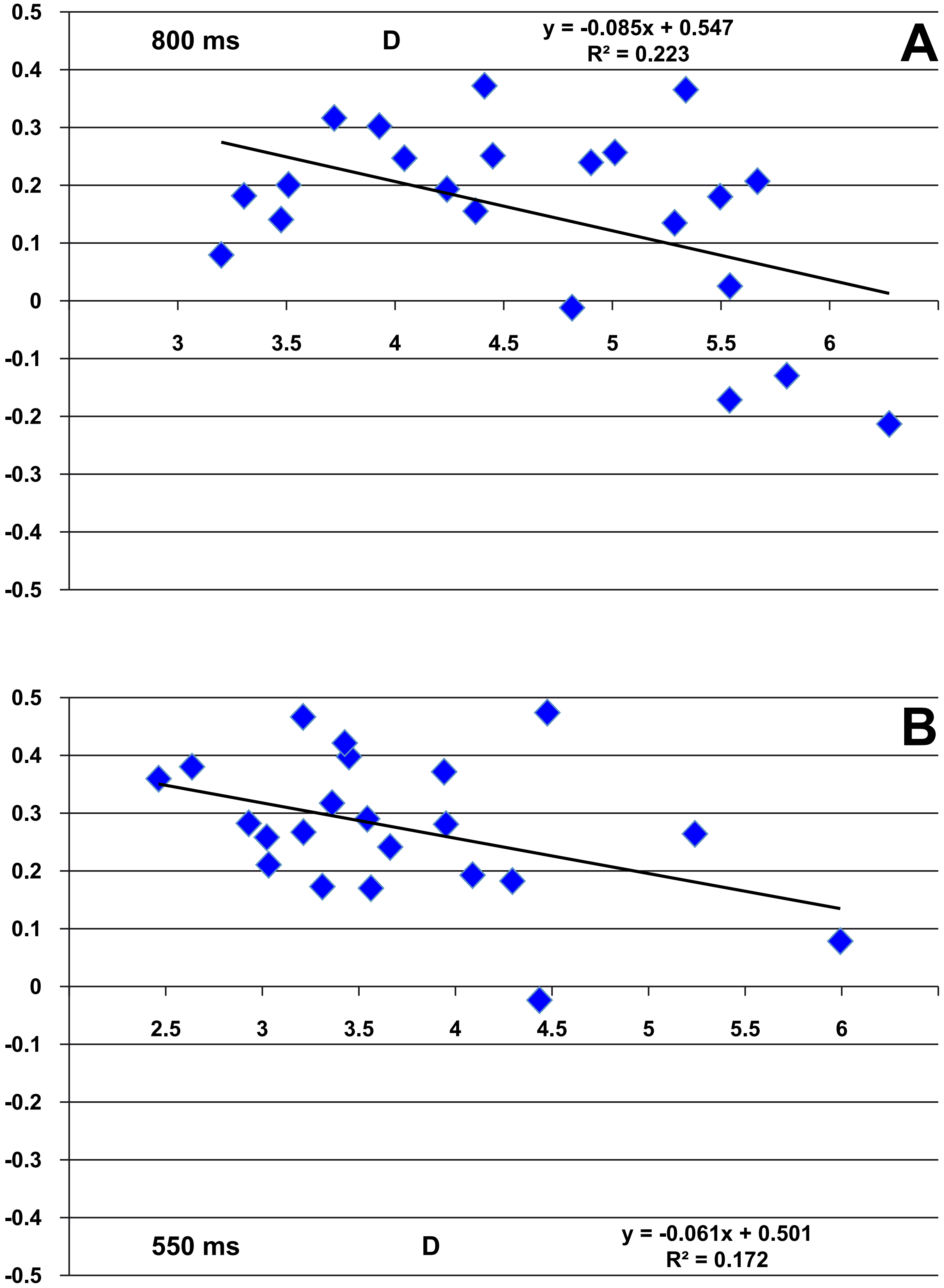

A
800 ms
D
y = -0.085x + 0.547
R² = 0.223
0.5
0.4
0.3
0.2
0.1
0
-0.1
-0.2
-0.3
-0.4
-0.5
3
3.5
4
4.5
5
5.5
6
B
550 ms
D
y = -0.061x + 0.501
R² = 0.172
0.5
0.4
0.3
0.2
0.1
0
-0.1
-0.2
-0.3
-0.4
-0.5
2.5
3
3.5
4
4.5
5
5.5
6

Figure 24

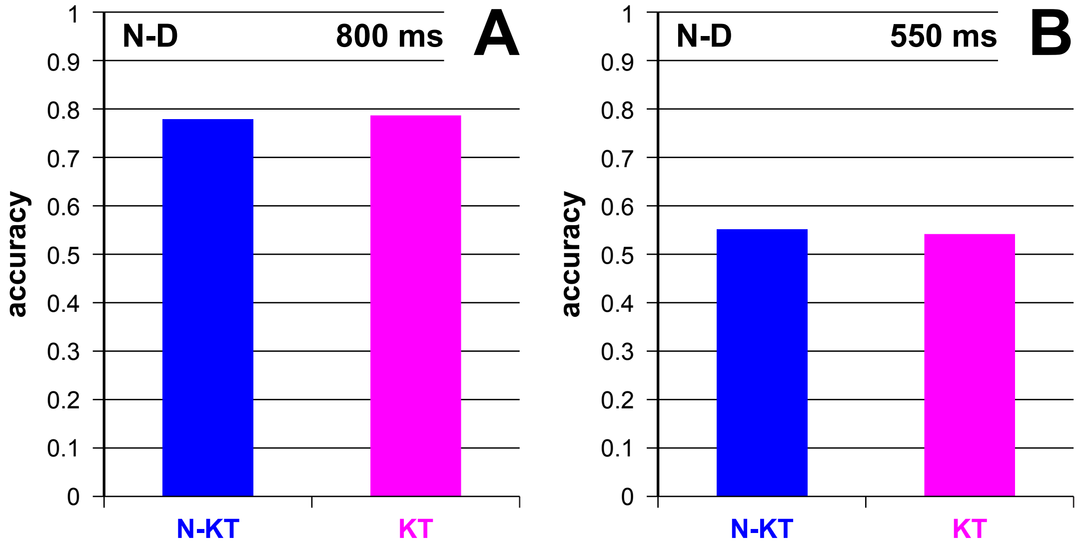

1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
accuracy
N-D
800 ms
A
N-KT
KT
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
accuracy
N-D
550 ms
B
N-KT
KT

Figure 25

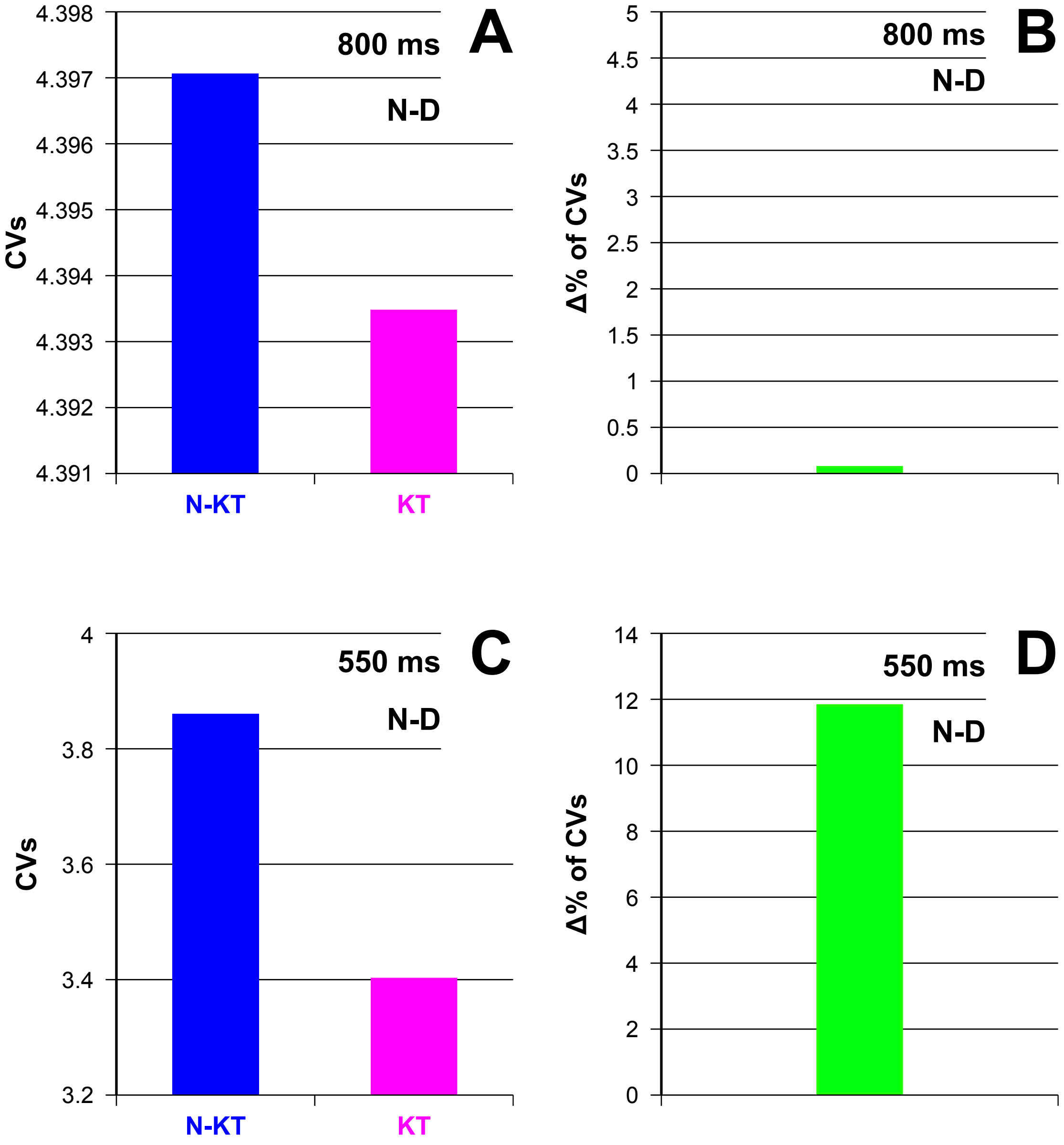

A
800 ms
N-D
CVs
4.398
4.397
4.396
4.395
4.394
4.393
4.392
4.391
N-KT
KT
B
800 ms
N-D
Δ% of CVs
5
4.5
4
3.5
3
2.5
2
1.5
1
0.5
0
C
550 ms
N-D
CVs
4
3.8
3.6
3.4
3.2
N-KT
KT
D
550 ms
N-D
Δ% of CVs
14
12
10
8
6
4
2
0

Figure 26

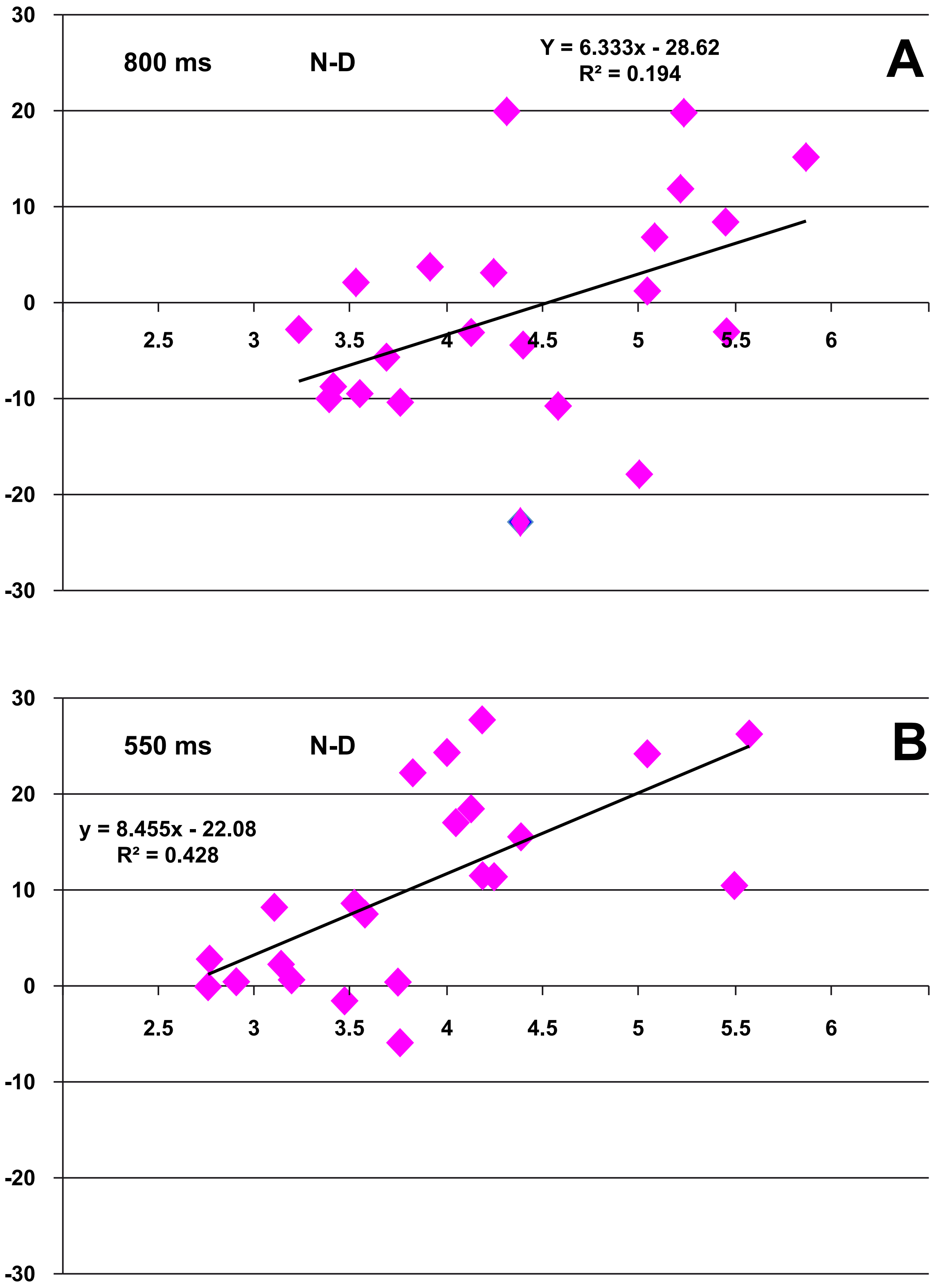

30
20
10
0
-10
-20
-30
800 ms
N-D
Y = 6.333x - 28.62
R² = 0.194
A
2.5
3
3.5
4
4.5
5
5.5
6
30
20
10
0
-10
-20
-30
550 ms
N-D
y = 8.455x - 22.08
R² = 0.428
B
2.5
3
3.5
4
4.5
5
5.5
6

Figure 27

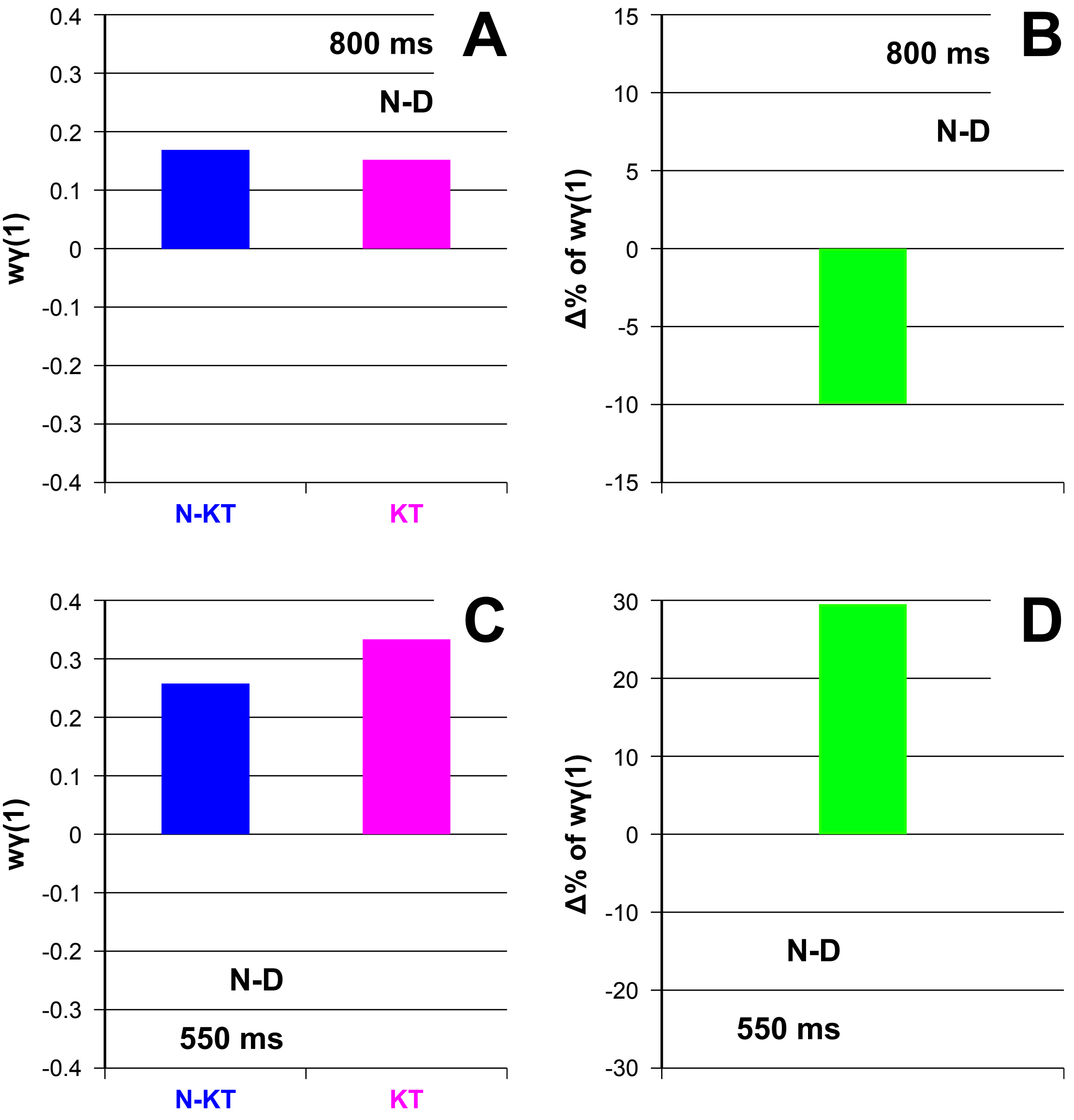

A
800 ms
N-D
wγ(1)
0.4
0.3
0.2
0.1
0
-0.1
-0.2
-0.3
-0.4
N-KT
KT
B
800 ms
N-D
Δ% of wγ(1)
15
10
5
0
-5
-10
-15
C
N-D
550 ms
wγ(1)
0.4
0.3
0.2
0.1
0
-0.1
-0.2
-0.3
-0.4
N-KT
KT
D
N-D
550 ms
Δ% of wγ(1)
30
20
10
0
-10
-20
-30

Figure 28

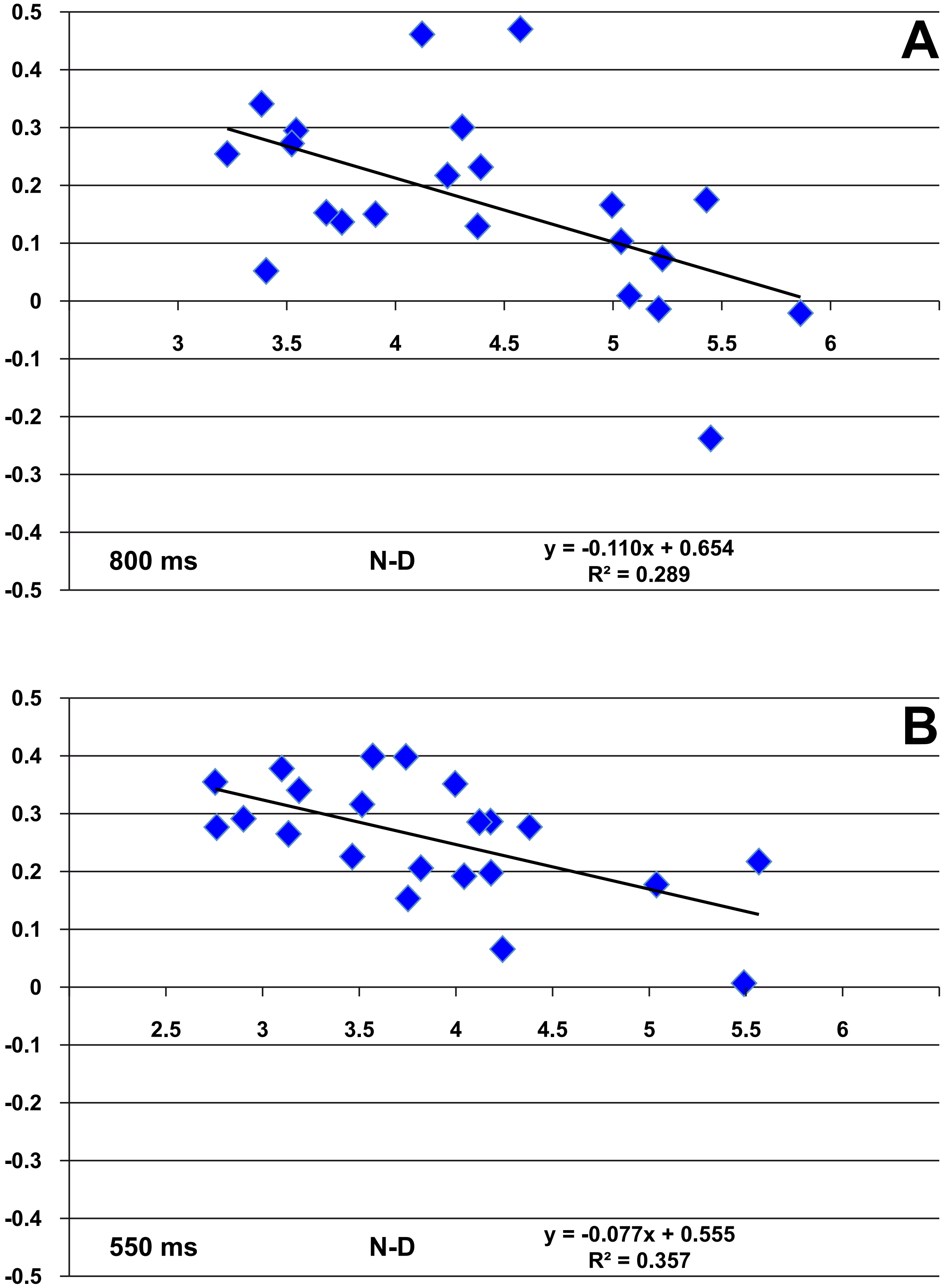

0.5
0.4
0.3
0.2
0.1
0
-0.1
-0.2
-0.3
-0.4
-0.5
A
3
3.5
4
4.5
5
5.5
6
800 ms
N-D
y = -0.110x + 0.654
R² = 0.289
0.5
0.4
0.3
0.2
0.1
0
-0.1
-0.2
-0.3
-0.4
-0.5
B
2.5
3
3.5
4
4.5
5
5.5
6
550 ms
N-D
y = -0.077x + 0.555
R² = 0.357

Figure 29

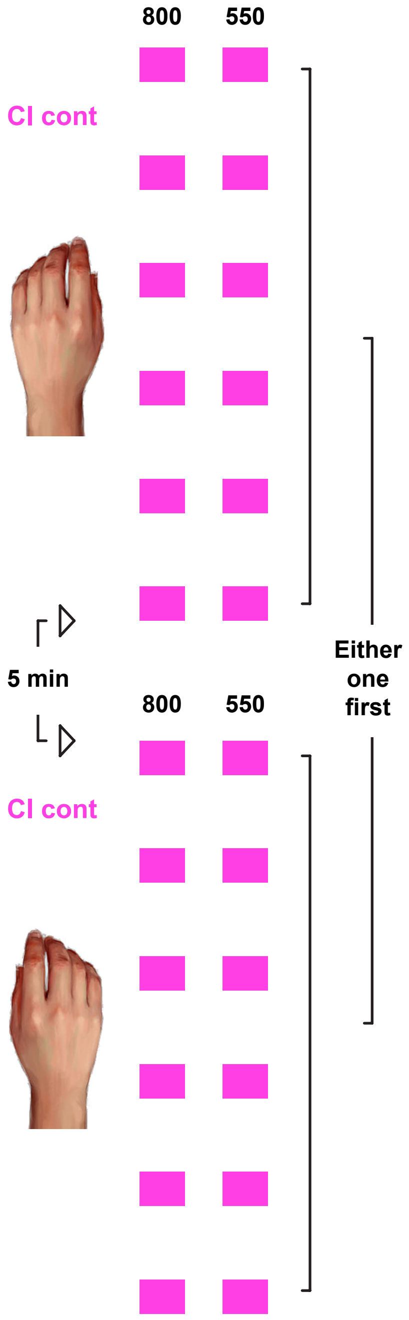


Figure 30

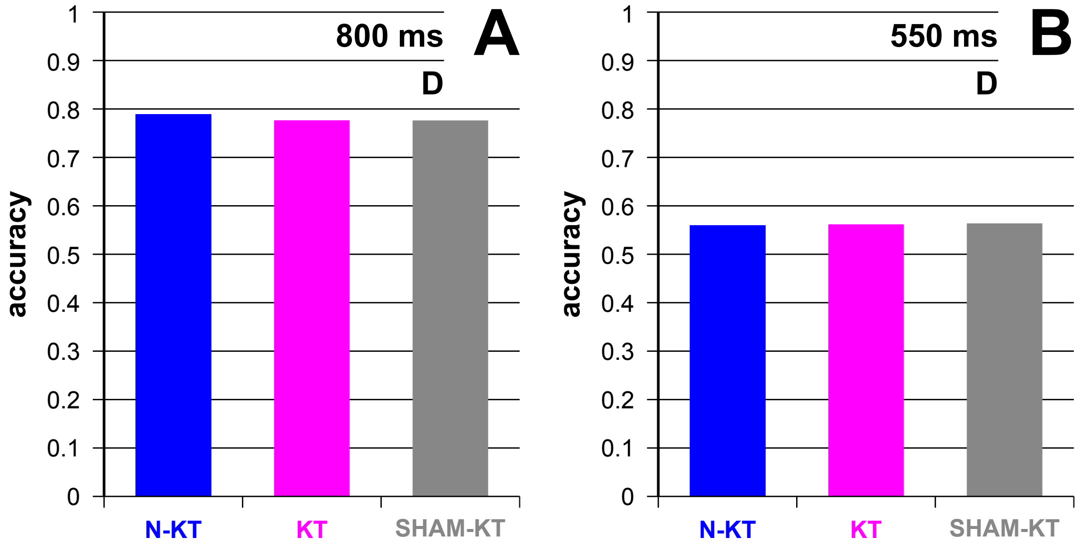

A
800 ms
D
accuracy
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
N-KT
KT
SHAM-KT
B
550 ms
D
accuracy
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
N-KT
KT
SHAM-KT

Figure 31

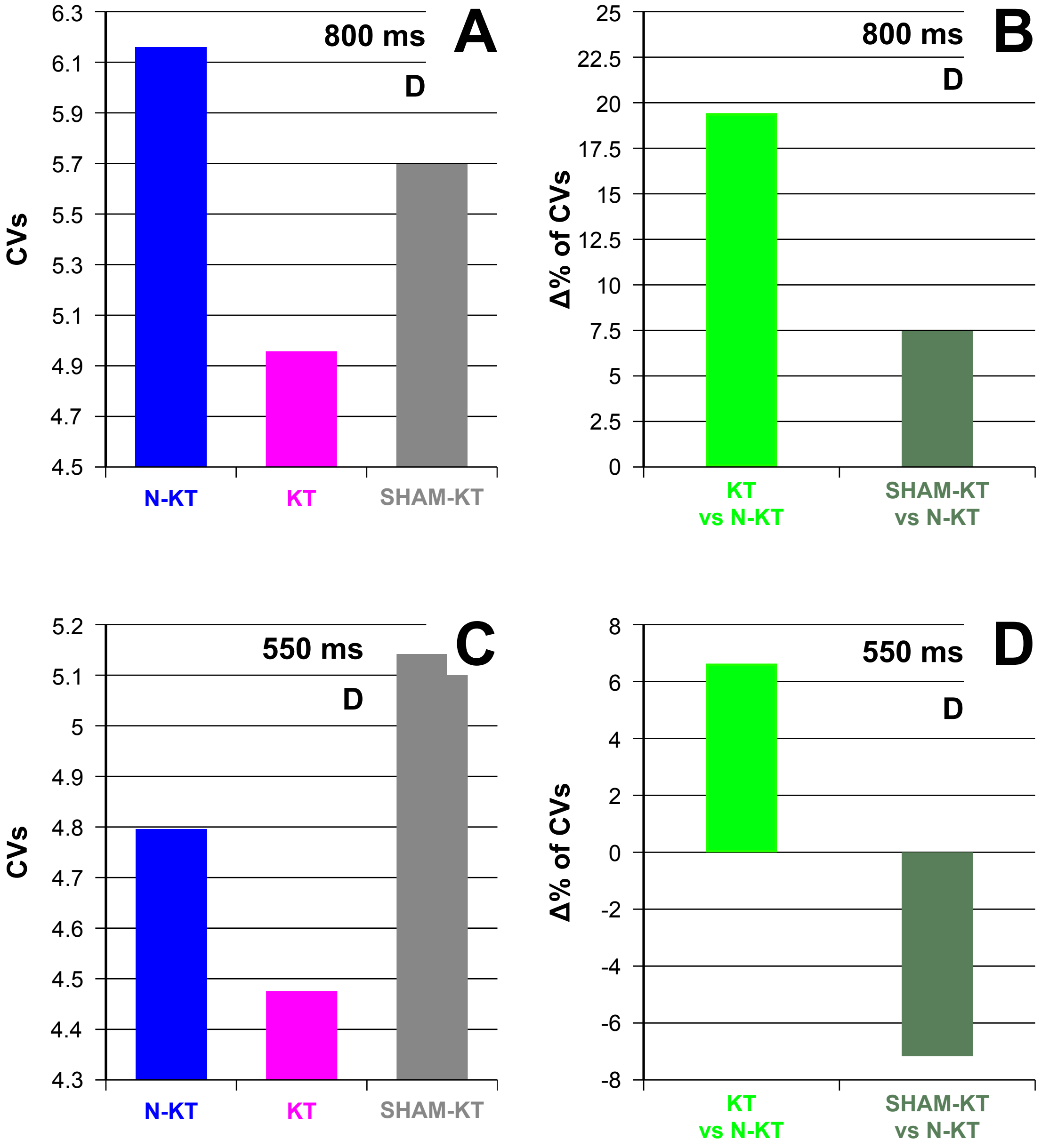

A
800 ms
D
CVs
6.3
6.1
5.9
5.7
5.5
5.3
5.1
4.9
4.7
4.5
N-KT
KT
SHAM-KT
B
800 ms
D
Δ% of CVs
25
22.5
20
17.5
15
12.5
10
7.5
5
2.5
0
KT vs N-KT
SHAM-KT vs N-KT
C
550 ms
D
CVs
5.2
5.1
5
4.9
4.8
4.7
4.6
4.5
4.4
4.3
N-KT
KT
SHAM-KT
D
550 ms
D
Δ% of CVs
8
6
4
2
0
-2
-4
-6
-8
KT vs N-KT
SHAM-KT vs N-KT

Figure 32

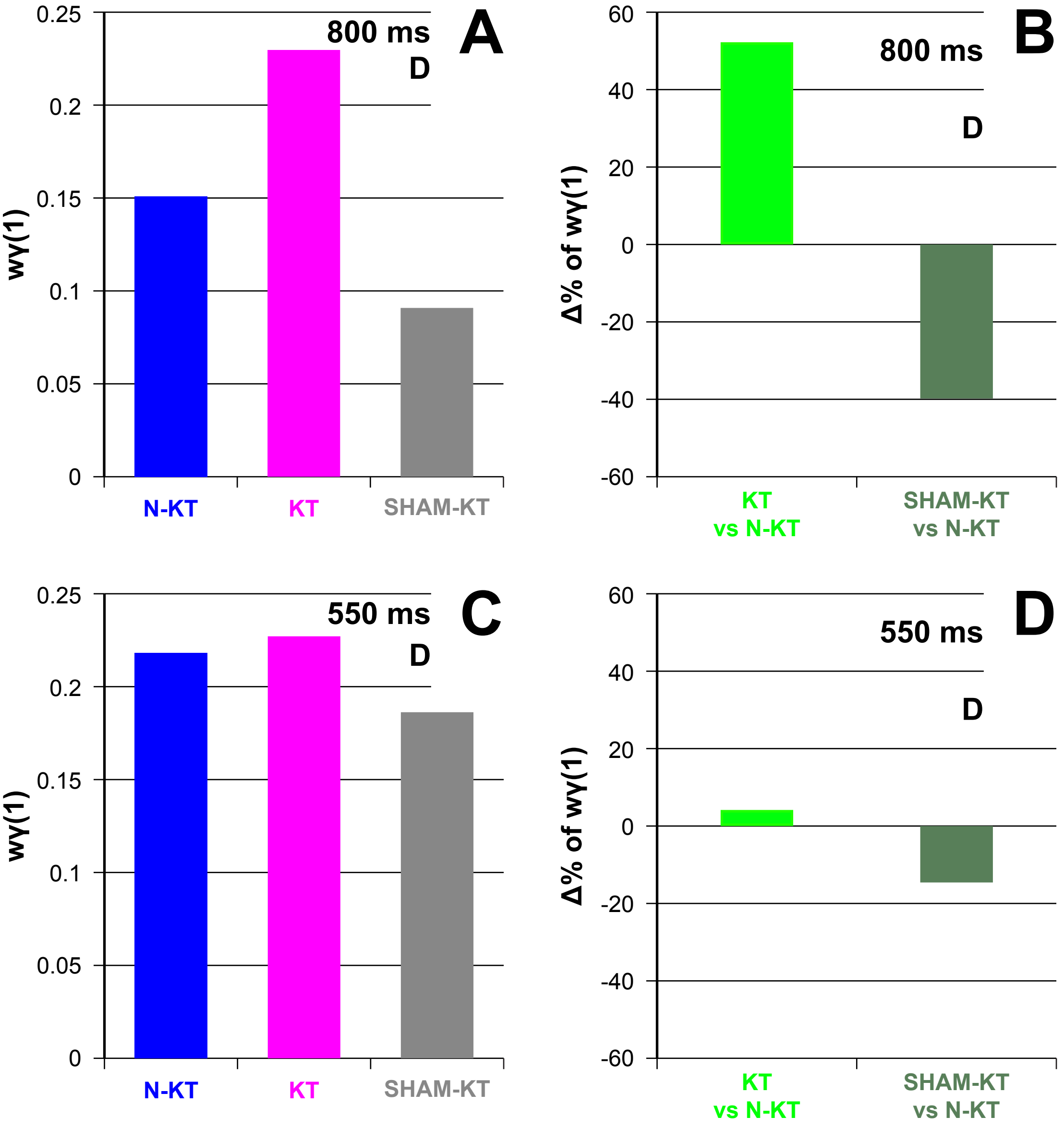
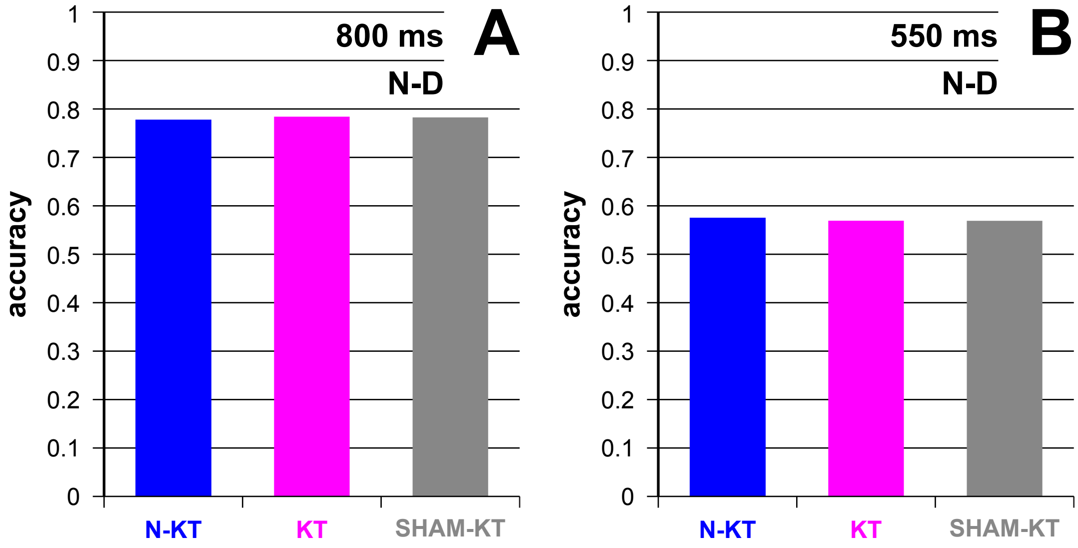

A
800 ms
D
wγ(1)
0.25
0.2
0.15
0.1
0.05
0
N-KT
KT
SHAM-KT
B
800 ms
D
Δ% of wγ(1)
60
40
20
0
-20
-40
-60
KT vs N-KT
SHAM-KT vs N-KT
C
550 ms
D
wγ(1)
0.25
0.2
0.15
0.1
0.05
0
N-KT
KT
SHAM-KT
D
550 ms
D
Δ% of wγ(1)
60
40
20
0
-20
-40
-60
KT vs N-KT
SHAM-KT vs N-KT

Figure 33



A
800 ms
N-D
B
550 ms
N-D
accuracy
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1
N-KT
KT
SHAM-KT

Figure 34

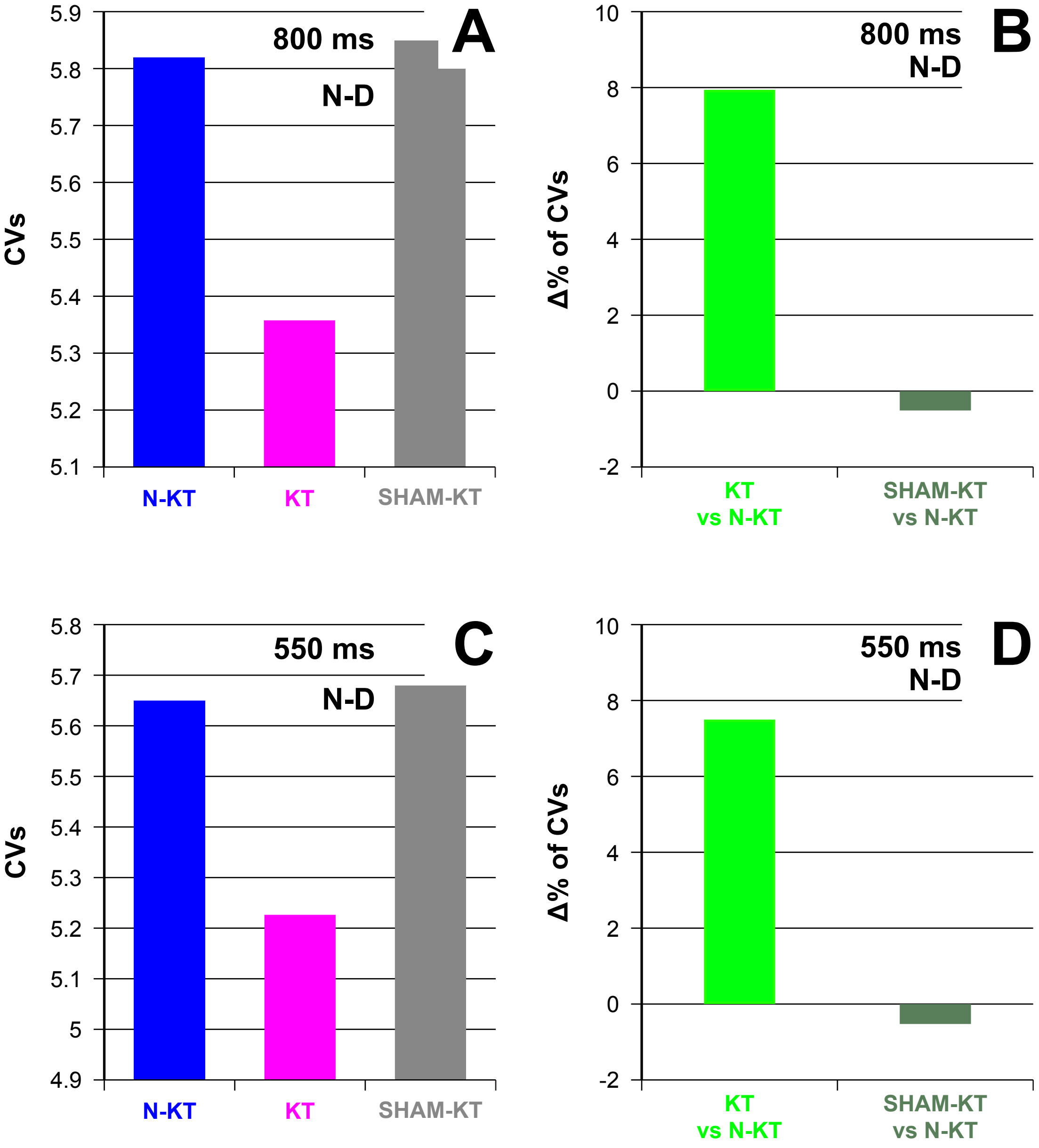

A
800 ms
N-D
CVs
5.9
5.8
5.7
5.6
5.5
5.4
5.3
5.2
5.1
N-KT
KT
SHAM-KT
B
800 ms
N-D
Δ% of CVs
10
8
6
4
2
0
-2
KT vs N-KT
SHAM-KT vs N-KT
C
550 ms
N-D
CVs
5.8
5.7
5.6
5.5
5.4
5.3
5.2
5.1
5
4.9
N-KT
KT
SHAM-KT
D
550 ms
N-D
Δ% of CVs
10
8
6
4
2
0
-2
KT vs N-KT
SHAM-KT vs N-KT

Figure 35

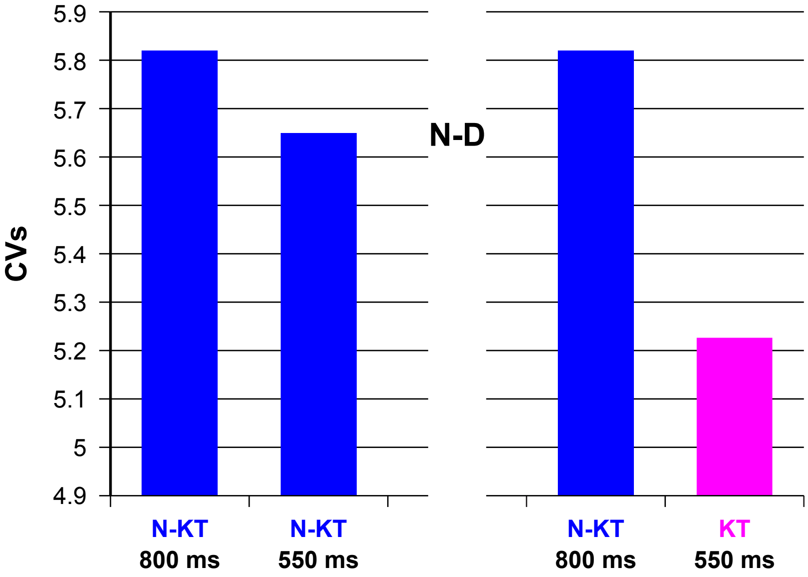

5.9
5.8
5.7
5.6
5.5
5.4
5.3
5.2
5.1
5
4.9
CVs
N-D
N-KT
800 ms
N-KT
550 ms
N-KT
800 ms
KT
550 ms

Figure 36

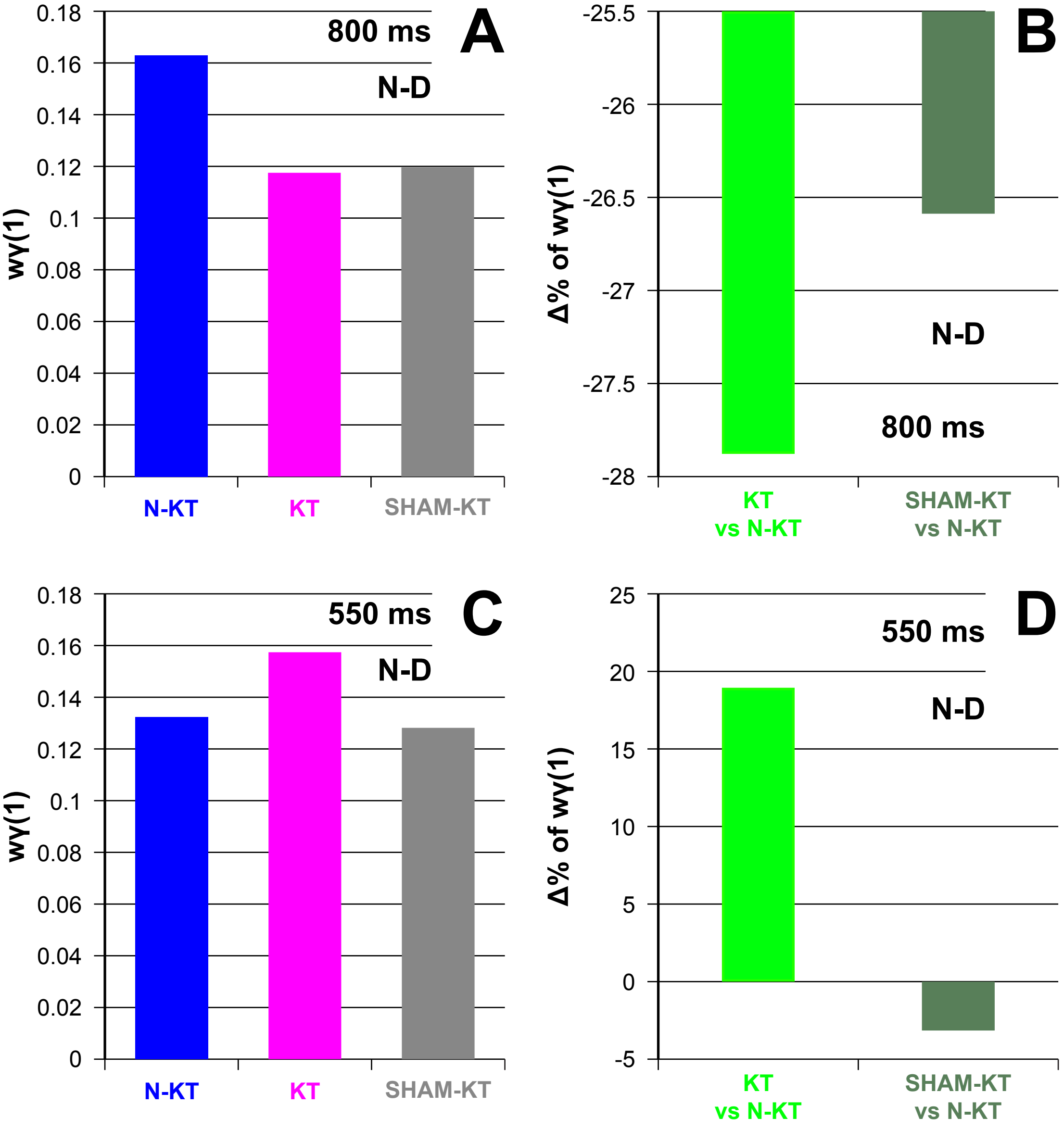

A
800 ms
N-D
wγ(1)
0.18
0.16
0.14
0.12
0.1
0.08
0.06
0.04
0.02
0
N-KT
KT
SHAM-KT
B
Δ% of wγ(1)
-25.5
-26
-26.5
-27
-27.5
-28
N-D
800 ms
KT vs N-KT
SHAM-KT vs N-KT
C
550 ms
N-D
wγ(1)
0.18
0.16
0.14
0.12
0.1
0.08
0.06
0.04
0.02
0
N-KT
KT
SHAM-KT
D
550 ms
N-D
Δ% of wγ(1)
25
20
15
10
5
0
-5
KT vs N-KT
SHAM-KT vs N-KT

Figure 37

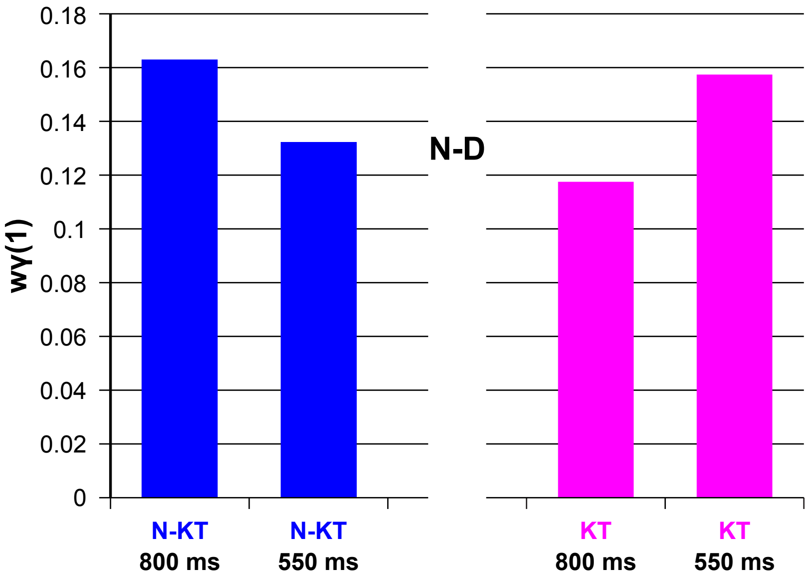

0.18
0.16
0.14
0.12
0.1
0.08
0.06
0.04
0.02
0
wγ(1)
N-D
N-KT
800 ms
N-KT
550 ms
KT
800 ms
KT
550 ms

Figure 38

Fig. 1 A, The subject is seated on a chair with an armrest, wearing a blindfold and headphones. The triaxial accelerometer is placed over the 2nd-3rd metacarpal bones. Subject is asked to perform sets of IWFEs (blue arrows). **B,** Audio information is presented as streams of clicks and excerpts of music. In the free condition audio is not presented. Spectrograms are obtained with the open source application Sonic Visualiser (dB Full Scale = dBFS; Cannam et al., 2010). **C,** The duration of each wrist's flexion-extension is calculated as difference between consecutive minima (red double headed arrow and marks). **D,** Sessions are designed to record first IWFEs in conditions free from auditory information (3 sets) and then in conditions related to listening of clicks followed by those related to listening of music (upper row, 6 sets), or vice versa (lower row, 6 sets). In this figure and in the following, the conditions and associated results are color-coded when illustrated in graphics (baseline recording, free = Fr; during the listening of clicks = Cl; recall after 2 minutes from the end of the Cl condition = Cl2; recall after 5 minutes from the end of the Cl condition = Cl5; during the listening of music = Mu; recall after 2 minutes from the end of the Mu condition = Mu2; and recall after 5 minutes from the end of the Mu condition = Mu5).

Fig. 2 A, B, C, Average within-ranges durations of our IWFEs are represented as function of average within-ranges SDs for the seven experimental conditions. The amount of dispersion is correlated to durations: slow movements have a greater variability than fast movements. **D,** CVs values of IWFEs durations are similar across conditions (columns = average within-condition CVs values, bars = average within-condition SDs). Note the small but visible difference between the conditions Fr, Cl, and Mu and the recall conditions Cl2, Cl5, Mu2, and Mu5.

Fig. 3 IWFEs tempi in the recall Cl2, Cl5, Mu2, and Mu5 conditions are illustrated as percent differences between the tempo performed in recall conditions and the reference tempo of the auditory stimulus. Percent differences of performed tempi are plotted versus ranges of tempi of the referred auditory input. After listening to clicks, in both Cl2 and Cl5 conditions, the IWFEs sets are performed at tempi faster than those of the original audio. Conversely, after listening to music, in both Mu2 and Mu5 conditions, subjects preferentially perform IWFEs sets at slower tempi. Dots = averages; bars = SDs.

Fig. 4 A, Audio information is presented as streams of clicks and excerpts of music. Spectrograms are obtained with the open source application Sonic Visualiser (dB Full Scale dBFS; Cannam et al., 2010). In the free and recall conditions, audio is not presented. **B,** The session is designed to record first IWFEs in a condition free from auditory constrain (in the absence of auditory information, free = Fr, self-paced = SP; faster than SP = >SP; faster than >SP = >>SP; slower than SP = <SP, see text for more details) and then in conditions related to clicks (during the listening of clicks = Cl; recall after 2 minutes from the end of the Cl condition = Cl2; one block consisting of two pairs of Cl and Cl2 sets performed at two different reference tempi: RT1 and RT2) followed by those related to music (during the listening of music = Mu; recall after 2 minutes from the end of the Mu condition = Mu2; one block consisting of two pairs of Mu and Mu2 sets performed at two different reference tempi: RT1 and RT2), or vice versa. In all figures the conditions and the associated results are color-coded.

Fig. 5 A, Mean w$\gamma(1)$ values (±SD) from the sets of IWFEs performed in the Fr, and during the listening of streams of clicks or excerpts of music, Cl and Mu, are plotted per condition, pooling together all ranges of tempi. Note that mean w$\gamma(1)$ is slightly positive for Fr, negative for Cl, and slightly negative for Mu. **B,**

Percentages of positive wγ(1) (±SD) in the Fr, Cl and Mu, are plotted per condition, pooling together all ranges of tempi. Note that the value for Fr is above 60% while for Cl and Mu the value is under 40%.

Fig. 6 **A,** Mean wγ(1) values of IWFEs are plotted, as a function of the ranges of tempi, for the Fr, Cl, and Mu conditions. Values change with movement durations. In the Fr condition mean wγ(1) values are almost all positive. In the Cl condition mean wγ(1) values are all negative. The Mu condition expresses positive values for fast movements, from ranks 10 to 15. **B,** Percentages of positive wγ(1) are plotted, as a function of the ranges of tempi, for the Fr, Cl, and Mu conditions. Also here it appears evident that percentages of positive wγ(1) values are sensitive to movement durations. In the Fr condition percentages of positive wγ(1) are almost always above 50%. In the Cl condition percentages of positive wγ(1) are under 50% for almost all ranks of tempi. In the Mu condition percentages of positive wγ(1) are above 50% at the high ranks (10 to 15). **C,** Inset of A. **D,** Inset of B.

Fig. 7 **A,** Mean wγ(1) values (±SD) from the sets of IWFEs are plotted pooling together all ranges of tempi for the recall Cl2 and Mu2 conditions (Fr is illustrated for reference). Note that mean wγ(1) values are slightly positive for Fr and somewhat negative for Cl2 and Mu2. **B,** Percentages of positive wγ(1) values (±SD) are plotted pooling together all ranges of tempi for the recall Cl2 and Mu2 conditions (Fr is illustrated for reference). Note that the value for Cl2 and Mu2 is under 50%.

Fig. 8 **A,** Mean wγ(1) values of IWFEs are plotted, as a function of the ranges of tempi, for the Cl2 and Mu2 conditions (Fr is illustrated for reference). Values change with movement durations. **B,** Percentages of positive wγ(1) are plotted, as a function of the ranges of tempi, for Cl2 and Mu2 conditions (Fr is illustrated for reference). Here also it is evident that percentages of positive wγ(1) are sensitive to movement durations. **C,** Inset of A. **D,** Inset of B.

Fig. 9 Data used to perform ANOVA analyses are shown. Columns are organized per rank; ranks 1 to 5 are illustrated. Wγ(1) values for slower movements on top and wγ(1) values for faster movements on bottom. For each graph the x-axis represents the order number of the window (window #) over which the autocorrelation is computed. Columns of graphs are referring, from left to right, to wγ(1) values in the conditions Fr, Cl, Mu, Cl2, and Mu2.

Fig. 10 Data used to perform ANOVA analyses are shown. Columns are organized per rank; ranks 6 to 10 are illustrated. All other parameters are the same as in the previous Figure.

Fig. 11 Data used to perform ANOVA analyses are shown. Columns are organized per rank; ranks 11 to 15 are illustrated. All other parameters are the same as in Figure 9.

Fig. 12 **A,** The subject is seated on a chair with armrests, wearing an eye-mask and headphones. The triaxial accelerometer is placed over the 2nd-3rd metacarpal bones. Subject is asked to perform sets of IWFEs. **B,** The two sessions, one with N-KT and one with KT (color-coded in pink) are designed to record first IWFEs in condition free from auditory information (in the absence of auditory information, free = Fr, self-paced = SP; slower than SP = <SP; faster than SP = >SP; faster than >SP = >>SP) and then in conditions related to clicks (during the listening of clicks = Cl; recall after 2 minutes from the end of the Cl condition = Cl2; one block consisting of three pairs of Cl and Cl2 sets performed at three different reference tempi: RT1, RT2, and RT3) followed by those related to music (during the listening of music = Mu; recall after 2 minutes from the end of the Mu condition = Mu2; one block consisting of three pairs Mu and Mu2 sets performed at three different reference tempi: RT1, RT2, and RT3), or vice versa. In this and in the following figures the conditions and associated results are color-coded. **C,** KT was placed between the lateral epicondyle of the humerus and phalanges, at the position of maximum flexion. **D,** KT was applied over the extensor carpi ulnaris, extensor carpi radialis longus and brevis, extensor digitorum, extensor indicis, extensor digiti minimi, and extensor pollicis longus. **E,** Proximally, KT was placed from 5 cm proximal to muscles insertion. **F,** Each branch of tape was applied down on the back of phalanx until the nail. As in the N-KT set up, the accelerometer was placed on the dorsal aspect of the hand, over the proximal part of the 2nd-3rd metacarpal bones, into a pocket kept in position by an elastic band and secured by a Velcro strap.

Fig. 13 A, B, Box plots of the response variable, i.e., the difference between the observed and the expected interval durations, for datasets in the conditions Mu and Mu2, respectively. Pairs of N-KT - KT box plots are noticeably similar when compared for slow (≥517.33 msec) versus fast (<517.33 msec) IWFEs durations. Also, easily appreciable is that the median, the upper and lower hinges and the whiskers are very similar for pairs of N-KT - KT parallel box plots in slow and fast collections of IWFEs durations. Conversely, the queues of the distributions are reduced when KT is applied (the only exception is a single far out value in the condition Mu2 for slow IWFEs with KT). KT reduces the variability of IWFEs durations.

Fig. 14 A-E, For each condition the CVs of IWFEs durations, ranked per within-ranges of durations, are illustrated. **F,** The five within-condition CVs of IWFEs durations are compared for N-KT and KT. **G,** The percent reduction of the within-condition CVs values when KT is applied. The reduction is more than 3% in all conditions; the most evident reduction, more than 10%, is for the Cl condition. Values are plotted as black (N-KT) and pink (KT) outlined circles, filled-in color-coded per condition. Color-coded connecting lines are shown to ease reading. CVs = within-range or, in F, within-condition CVs values. WRMD = within-ranges movements durations.

Fig. 15 A, B, Mean windowed wγ(1) values, ranked per within-ranges of durations, are illustrated. The conditions Cl and Cl2 are compared for N-KT and KT. Note that mean wγ(1) values appear to change with movement durations and are, for both Cl and Cl2 conditions, biased toward more positive values when KT is applied. Values are plotted as black (N-KT) and pink (KT) outlined circles, filled-in color-coded per condition. WRMD = within-ranges movements durations.

Fig. 16 A-D, On the radar charts are illustrated, for the N-KT and KT cases of Cl and Cl2 conditions, the percentages of positive and negative wγ(1) values ranked per within-ranges of durations. Note that the areas generated by the eight within-range percentages of positive wγ(1) values are wider in the KT than in N-KT cases for both Cl and Cl2 conditions. **E-F,** The percentages of N-KT versus KT positive wγ(1) values are compared for the Cl and the Cl2 conditions, respectively. The red area indicates for each of the eight within-ranges of durations the differential percent of positive wγ(1) values. This area is wider in the KT than in the N-KT case, both for the Cl and the Cl2 conditions. Compound shapes are obtained by combination of areas of positive wγ(1) values in the N-KT and KT cases for both the Cl and Cl2 conditions. The overlapping area was excluded, turning the filled region into a hole. **G,** The increase of positive wγ(1) values in the KT case is comprehensively indicated as differential percent equivalent both for the Cl and Cl2 conditions (see text for more explanations). %pos (red) = percentages of positive wγ(1) values. %neg (black) = percentages of negative wγ(1) values. δ%pos (red) = differential percent equivalent for percentages of positive wγ(1) values. δ%neg (black) = differential percent equivalent for percentages of negative wγ(1) values.

Fig. 17 **A,** The participant, sitting upright on a chair, placed the dominant forearm on armrest, in a relaxed horizontal position. The triaxial accelerometer was placed on the dorsal aspect of the hand, over the proximal part of the 2nd–3rd metacarpal bones. The participant was asked to keep the wrist and forearm in full flexion and full pronation. **B,** The facilitatory KT - from origin to insertion (arrow) - application was performed, with the light 25% tension (fKT). **C,** The facilitatory KT - from origin to insertion (arrow) - was performed, with the moderate 50% tension (fKT-T). **D,** The inhibitory KT - from insertion to origin (arrow) - was performed, with the moderate 25% tension (iKT). E, Each session consisted of 16 sets of repeated IWFEs, 8 performed synchronized to streams of clicks with IOI of 500 ms and 8 to streams of clicks with IOI of 400 ms. The streams of clicks (Cl) had a duration of 60 s. The sets of IWFEs were separated by 45 s rests to avoid fatigue during performance.

Fig. 18 The SDasy and the percentage difference (Δ%) of the SDasy while synchronizing movements to streams of clicks having IOI of 500 and 400 ms. **A,** For IOI of 500 ms, absolute values of SDasy are remarkably different between without KT (N-KT) and the other KT cases. **B,** Δ% of the SDasy for IOI of 500 ms is measured as percentage differences between every single case in which KT was applied and the N-KT case. Note that improvement of precision is evident in all KT cases. **C,** Also for the IOI of 400 ms, the absolute value of SDasy in the

N-KT case is higher than in the KT cases. **D,** Δ% of the SDasy for IOI of 400 ms. Note that here also there is an improvement of precision in all KT cases. Other abbreviations as in Figure 17.

Fig. 19 Each session consisted of 32 sets of repeated isochronous wrist's flexion-extensions (IWFEs), whose 16 sets with each hand. Eight sets were performed unimanually at each of two interval durations conditions (550 and 800 ms). The sets of IWFEs were separated by 45 s rests to avoid fatigue during performance.

Fig. 20 A, B, The accuracy in N-KT and KT cases, for 800 and 550 ms conditions.

Fig. 21 The CVs of IWFEs and the percentage difference (Δ%) of CVs in 800 and 550 ms conditions. CV and Δ% of CVs are to be considered as the case's means. **A,** In the 800 ms condition, CVs are not different between N-KT and KT cases. **B,** 800 ms condition Δ% of CVs is measured as percentage differences between KT and the N-KT cases. **C,** In the 550 ms condition, CV in N-KT case is higher than CV in KT case. **D,** Δ% of the of CVs in the 550 ms condition. KT improves the precision of IWFEs.

Fig. 22 A, B, Correlation of mean CVs values expressed in increasing order of magnitude, and obtained by each subject in N-KT case, with the respective Δ% of CVs value, for 800 and 550 ms conditions. KT has a greater effect when the subject performs IWFEs with higher temporal variability in N-KT case.

Fig. 23 The wγ(1) of IWFEs and the percentage difference (Δ%) of wγ(1) in the 800 and 550 ms conditions. Wγ(1) and Δ% of wγ(1) are to be considered as the case's means. **A,** In the 800 ms condition, wγ(1) are positive in N-KT and KT cases. **B,** In the 800 ms condition, Δ% of the wγ(1) is measured as percentage differences between N-KT and KT cases. The employment of the emergent timing component is shown to be reduced with KT. **C,** In the 550 ms condition, wγ(1) values were strikingly positive in N-KT and KT cases, and they were higher than those obtained in the 800 ms condition. **D,** The employment of the emergent timing component is shown to be enhanced with KT.

Fig. 24 A, B, Correlation of mean CVs values expressed in increasing order of magnitude, and obtained by each subject in N-KT case, with the own mean wγ(1) value, for 800 and 550 ms conditions. When timing performance presents a low temporal variability, the mean wγ(1) value tend to be remarkably positive.

Fig. 25 A, B, The accuracy in N-KT and KT cases, for 800 and 550 ms conditions.

Fig. 26 The CVs of IWFEs and the percentage difference (Δ%) of CVs in 800 and 550 ms conditions. CV and Δ% of CVs are to be considered as the case's means. **A,** In the 800 ms condition, CVs are not different between N-KT and KT cases. **B,** In 800 ms condition Δ% of CVs is measured as percentage differences between KT and the N-KT cases. **C,** In the 550 ms condition, CV in N-KT case is higher than CV in KT case. **D,** Δ% of the of CVs in the 550 ms condition. KT improves the precision of IWFEs.

Fig. 27 A, B, Correlation of mean CVs values expressed in increasing order of magnitude, and obtained by each subject in N-KT case, with the respective Δ% of CVs value, for 800 and 550 ms conditions. The effect of KT is greater, the more the subjects'timing performance presents high CV.

Fig. 28 The wγ(1) of IWFEs and the percentage difference (Δ%) of wγ(1) in the 800 and 550 ms conditions. Wγ(1) and Δ% of wγ(1) are to be considered as the case's means. **A,** In the 800 ms condition, wγ(1) are positive in N-KT and KT cases. **B,** In the 800 ms condition, Δ% of the wγ(1) is measured as percentage differences between N-KT and KT cases. The employment of the emergent timing component is shown to be reduced with KT. **C,** In the 550 ms condition, wγ(1) values are strikingly positive in N-KT and KT cases, and they are higher than those obtained in the 800 ms condition. **D,** The employment of the emergent timing component is shown to be enhanced with KT.

Fig. 29 A, B, Correlation of mean CVs values expressed in increasing order of magnitude, and obtained by each subject in N-KT case, with the own mean wγ(1) value, for 800 and 550 ms conditions. When timing performance presents a low temporal variability, the mean wγ(1) value tend to be remarkably positive.

Fig. 30 Each session consisted of 24 sets of repeated IWFEs, whose 12 sets with each hand. Six sets were performed unimanually at each of two interval durations conditions (550 and 800 ms).

Fig. 31 A, B, The accuracy in N-KT, KT, and KT-SHAM, in the 800 and 550 ms conditions.

Fig. 32 The CVs of IWFEs and the percentage difference (Δ%) of CVs in 800 and 550 ms conditions. CV and Δ% of CVs are to be considered as the case's means. **A,** In the 800 ms condition, CVs are remarkably different between N-KT, and the KT and SHAM-KT cases. **B,** In 800 ms condition Δ% of CVs is measured as percentage differences between every single case in which KT and KT-SHAM was applied and the N-KT case. It is to mention that the improvement of precision is evident in both KT and KT-SHAM cases. **C,** In the 550 ms condition, KT and KT-SHAM influence precision of IWFEs. **D,** Δ% of the CVs in the 550 ms condition. KT improves the precision of IWFEs, while KT-SHAM reduces it.

Fig. 33 The wγ(1) of IWFEs and the percentage difference (Δ%) of wγ(1) in the 800 and 550 ms conditions. Wγ(1) and Δ% of wγ(1) are to be considered as the case's means. **A,** In the 800 ms condition, wγ(1) are positive in N-KT, KT, and SHAM-KT cases. **B,** In the 800 ms condition Δ% of the wγ(1) is measured as percentage differences between every single case in which KT and KT-SHAM was applied and the N-KT case. The employment of the emergent timing component is shown to augmented with KT, while it is reduced by using SHAM-KT. **C,** In the 550 ms condition, wγ(1) values were strikingly positive in all cases, and they were higher than those obtained in the 800 ms condition. **D,** Wγ(1) is not influenced by KT, and it is slighty modified by SHAM-KT as shown from Δ%.

Fig. 34 A, B, The accuracy in the 800 and 550 ms conditions, in N-KT, KT, and KT-SHAM.

Fig. 35 The CVs of IWFEs and the percentage difference (Δ%) of CVs in the 800 and 550 ms conditions. CV and Δ% of CVs are to be considered as the case's means. **A,** In the 800 ms condition, unlike SHAM-KT, KT application influences CV value **B,** In 800 ms condition, Δ% of CVs is measured as percentage differences between every single case in which KT and KT-SHAM was applied and the N-KT case. It is to mention that the improvement of precision is evident only when KT is applied. **C,** In the 550 ms condition, unlike SHAM-KT, KT application influences CV value. **D,** Note that also here there is an improvement of precision only when KT is applied.

Fig. 36 Mean CVs of IWFEs achieved in both time conditions (800 and 550 ms, respectively) in N-KT case, and mean CV of IWFEs achieved in the 550 ms time condition in the N-KT and KT case. It is to mention that KT, by reducing the CV value in the 550 ms condition, recreates the physiological constant ratio of the standard deviation divided by the timed interval across the two different intervals.

Fig. 37 The wγ(1) of IWFEs and the percentage difference (Δ%) of wγ(1) in the 800 and 550 ms conditions. Wγ(1) and Δ% of wγ(1) are to be considered as the case's means. **A,** In the 800 ms condition, the mean wγ(1) is positive in N-KT, KT and SHAM-KT. **B,** The employment of the emergent timing component is reduced both when KT and KT-SHAM are applied. **C,** In the 550 ms condition, wγ(1) values are positive in N-KT, KT, and SHAM-KT. **D,** The employment of the emergent timing component is augmented only by the use of KT.

Fig. 38 Mean wγ(1) values of IWFEs achieved in both KT and N-KT cases for both time conditions (800 and 550 ms, respectively). It is to mention that KT, by reducing the CV value in the 550 ms condition, recreates phisiological trend observed in healthy subjects, in whom it has been shown that the w$\gamma(1)$ values are higher the more the frequency of movements increases.

Tables

TABLE 1

Musical names, ranking, and tempo equivalences between ranges in beats per minute and Hertz

		Tempo equivalences					
Musical names	**Rank**	**Ranges in bpm (*)**			**Ranges in Hz**		
		reference	**from**	**to**	**reference**	**from**	**to**
Adagio	**1**	64	61	68	1.067	1.017	1.133
	2	72	69	76	1.200	1.150	1.267
Andante	**3**	80	77	84	1.333	1.283	1.400
	4	88	85	92	1.467	1.417	1.533
	5	96	93	100	1.600	1.550	1.667
	6	104	101	108	1.733	1.683	1.800
Moderato	**7**	112	109	116	1.867	1.817	1.933
	8	120	117	124	2.000	1.950	2.067
	9	128	125	132	2.133	2.083	2.200
Allegro	**10**	136	133	140	2.267	2.217	2.333
	11	144	141	148	2.400	2.350	2.467
	12	152	149	156	2.533	2.483	2.600
	13	162	157	168	2.700	2.617	2.800
Presto	**14**	176	169	180	2.933	2.817	3.000

(*) bpm = beats per minute

TABLE 2

Correlation coefficients of SDs versus IWFEs durations

Condition	**Pearson coef. (r)**
Fr	0.9902
Cl	0.9919
Cl2	0.9959
Cl5	0.9920
Mu	0.9931
Mu2	0.9906
Mu5	0.9806

TABLE 3

Musical names, ranking, and tempo equivalences among ranges in beats per minute, Hz and msec

Musical names	Rank	Tempo equivalences								
		Ranges (bpm)			Ranges (Hz)			Ranges (ms)		
		Reference	From	To	Reference	From	To	Reference	From	To
Adagio	**1**	64	61	68	1.067	1.017	1.133	937.207	983.284	882.613
	2	72	69	76	1.200	1.150	1.267	833.333	869.565	789.266
Andante	**3**	80	77	84	1.333	1.283	1.400	750.188	779.423	714.286
	4	88	85	92	1.467	1.417	1.533	681.663	705.716	652.316
	5	96	93	100	1.600	1.550	1.667	625.000	645.161	599.880
	6	104	101	108	1.733	1.683	1.800	577.034	594.177	555.556
Moderato	**7**	112	109	116	1.867	1.817	1.933	535.619	550.358	517.331
	8	120	117	124	2.000	1.950	2.067	500.000	512.821	483.793
	9	128	125	132	2.133	2.083	2.200	468.823	480.077	454.545
Allegro	**10**	136	133	140	2.267	2.217	2.333	441.112	451.060	428.633
	11	144	141	148	2.400	2.350	2.467	416.667	425.532	405.351
	12	152	149	156	2.533	2.483	2.600	394.789	402.739	384.615
	13	160	157	164	2.667	2.617	2.733	375.000	382.166	365.854
	14	168	165	172	2.800	2.750	2.867	357.143	363.636	348.837
Presto	**15**	176	173	180	2.933	2.883	3.000	340.910	346.821	333.333

TABLE 4

Musical names, ranking, and tempo equivalences between ranges of movement durations in Hertz and milliseconds

Musical names	**Rank**	**Tempo equivalences**					
		Ranges (Hz)			**Ranges (ms)**		
		Reference	**From**	**To**	**Reference**	**From**	**To**
Adagio	**1**	1.067	1.017	1.133	937.21	983.28	882.61
Andante	**2**	1.333	1.283	1.400	750.19	779.42	714.29
	3	1.600	1.550	1.667	625.00	645.16	599.88
Moderato	**4**	1.867	1.817	1.933	535.62	550.36	517.33
	5	2.133	2.083	2.200	468.82	480.08	454.55
Allegro	**6**	2.400	2.350	2.467	416.67	425.53	405.35
	7	2.700	2.617	2.800	370.37	382.12	357.14
Presto	**8**	2.933	2.817	3.000	340.95	354.99	333.33

TABLE 5

Estimate, *p*-values (in parenthesis) and confidence intervals for model parameters in random effects ANOVA models for the Cl and Mu conditions

Main fixed effects	**Cl**		**Mu**	
	Estimate (*p*-value)	**95% confidence Interval**	**Estimate (*p*-value)**	**95% confidence Interval**
Overall mean	-0.0063 (0.0000)	-0.0086; -0.0039	-0.0056 (0.0100)	-0.0099; -0.0013
Movement duration	0.0021 (0.0283)	0.0002; 0.0040	0.0042 (0.0401)	0.0002; 0.0083
N-KT versus KT	-0.0009 (0.3349)	-0.0009; 0.0026	-0.0020 (0.3004)	-0.0058; 0.0018

Random effects	**Estimate**	**95% confidence Interval**	**Estimate**	**95% confidence Interval**
Within-individual SD	0.0045	0.0032; 0.0064	0.0066	0.0042; 0.0101
Within-set SD	0.0049	0.0042; 0.0057	0.0115	0.0101; 0.131
KT residual variance ratio	0.8635	0.8440; 0.8835	0.9242	0.9036; 0.9452

TABLE 6

Factor specific residual variances (σ2) for N-KT versus KT movements

Condition	**N-KT** σ^2	**KT** σ^2	**N-KT vs KT** ***p*-value**
Cl	0.00076729	0.0006625549	<0.0001
Mu	0.000772	0.000714	<0.0001
Recalls (Cl2 and Mu2)	0.00085849	0.0008080108	<0.0001
Fr	0.00082369	0.0007996383	0.005

TABLE 7

Estimate, *p*-values (in parenthesis) and confidence intervals for model parameters in random effects ANOVA models for the Recalls and Fr conditions

	Recalls (Cl2 and Mu2)		Fr	
Main fixed effects	**Estimate (*p*-value)**	**95% confidence Interval**	**Estimate (*p*-value)**	**95% confidence Interval**
Overall mean	-0.0014 (0.7492)	-0.0071; -0.0099	0.7218 (0.0000)	0.6865; 0.7571
Movement duration	-0.0034 (0.4347)	-0.0121; 0.0052	-0.3147 (0.0000)	-0.3571; -0.2723
N-KT versus KT	0.0031 (0.4836)	-0.0055; 0.0117	0.0114 (0.5934)	-0.0306; 0.0533

Random effects	**Estimate**	**95% confidence Interval**	**Estimate**	**95% confidence Interval**
Within-individual SD	0.0031	1e-04; 0.0993	0.0127	1e-04; 1.2508
Within-set SD	0.0377	0.0347; 0.0410	0.1452	0.1306; 0.1614
KT residual variance ratio	0.9412	0.9252; 0.9575	0.9708	0.9511; 0.9908

TABLE 8

Population Data

	Diagnosis	Gender	Age	ICARS Total	Limb movement disturbances		postural and stance disturbances	Speech Disorders	Oculomotor Disorders
					Ataxia, Upper	**Ataxia, Lower**			
P1	SCA1	F	37	20	5	1	10	2	2
P2	SCA2	M	49	25	6	4	10	4	1
P3	SCA2	M	52	26	6	4	12	2	2
P4	Atrophy	M	69	26	6	5	11	3	1
P5	SCA2	M	76	32	9	3	18	2	0

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