MOVING, FAST AND SLOW: COGNITIVE CONTROL OF MOTOR TIMING EXAMINED THROUGH THE APPLICATION OF THE *f*NIRS TECHNOLOGY

BOUGER, VITE ET LENTEMENT : LE CONTRÔLE COGNITIF DE LA CHRONOMÉTRIE MOTRICE EXAMINÉ PAR L'APPLICATION DE LA TECHNOLOGIE *f*NIRS

A thesis submitted
by
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Ségolène M. R. Guérin: *Moving, Fast and Slow: Cognitive Control of Motor Timing Examined through the Application of the fNIRS Technology* © October 2021

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J'ai laissé des bouts de moi au creux de chaque endroit
Un peu de chair à chaque empreinte de mes pas

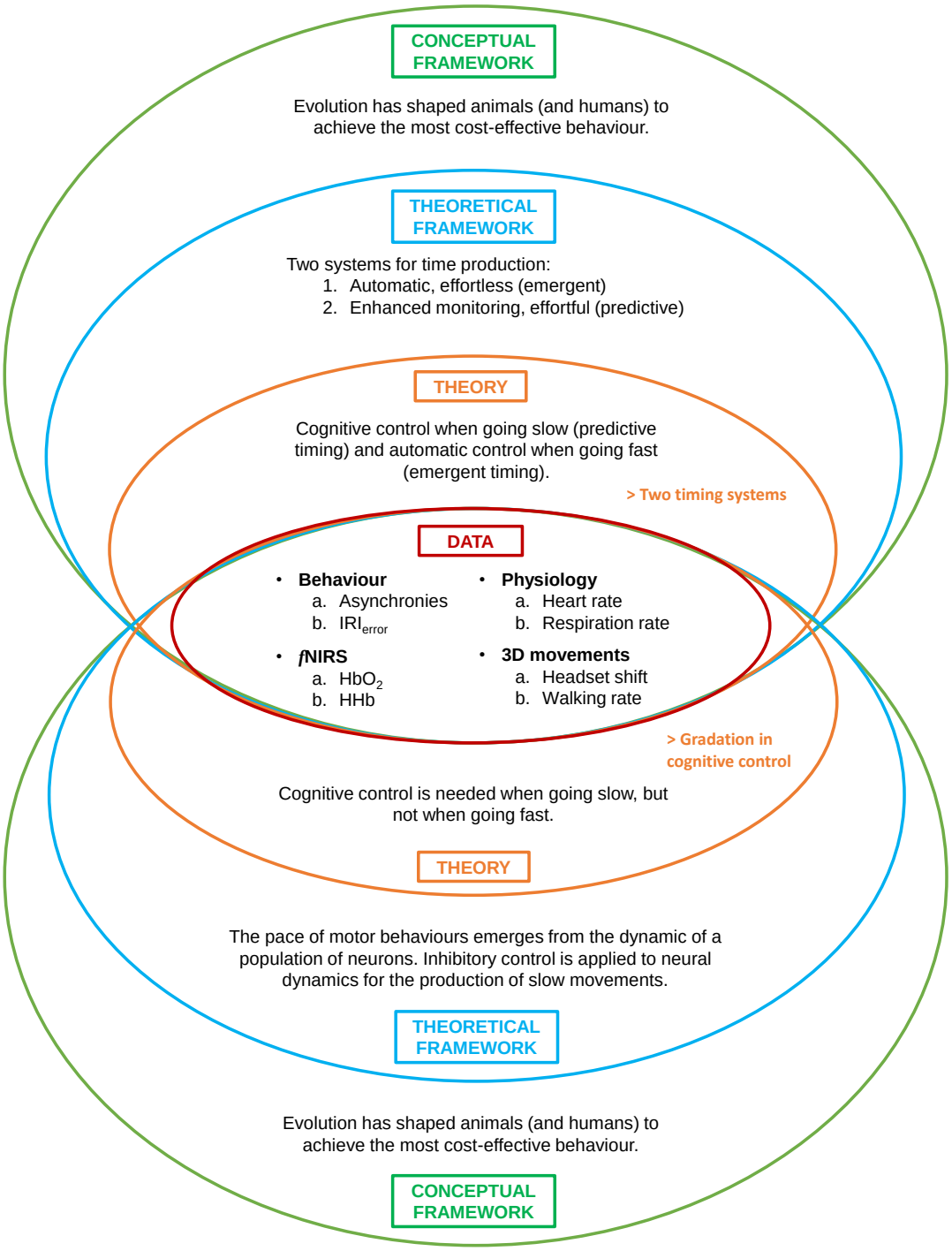
— Jean-Jacques Goldman

ABSTRACT

Human beings constantly adapt the spontaneous pace of their actions in order to interact with their environment. Advances in timing research have shown that two processes (automatic vs. controlled) are involved in the processing of temporal information. There is, nonetheless, a dearth of knowledge regarding the cognitive mechanisms and brain areas underlying the temporal control of motor behaviours. The general aim of my thesis was to examine the cognitive and cerebral resources needed during the execution of actions performed under different time constraints. In Study 1, the involvement of cognitive control in motor timing was investigated using time series analysis and a dual-task paradigm. Results showed that moving fast and slow entailed distinct timing strategies, characterised by contrasting attentional demands. In Study 2, the *f*NIRS neuroimaging technique was used to examine the cerebral oxygenation of prefrontal and motor areas simultaneously during the execution of upper-limb motor tasks performed under different time constraint. Findings indicated that fast-paced movement relied on greater activity in the motor areas, whereas moving at a close-to-spontaneous pace exerted heavier load on the posterior prefrontal cortex. Study 3 was designed to investigate the ecological validity of motor-timing tasks by providing a direct comparison across the tasks of finger tapping, foot tapping, and stepping on the spot. The results showed that single-limb and whole-body movements entailed distinct timing strategies, and suggested that tapping-to-metronome paradigms might be too far removed from natural behaviours to facilitate translation of the results. Hence, in Study 4, the *f*NIRS technique was employed to examine prefrontal and motor activation during the execution of upper-limb and whole-body movements under distinct time constraints. Findings indicated that slow pacing led to increased prefrontal activations only during whole-body movements. Yet, a large variability in participants' haemodynamic responses was observed. Therefore, in Study 5, three case studies were conducted to assess the test–retest reliability and define the appropriate number of trials necessary for a block design procedure in *f*NIRS brain imaging during motor paradigms. The original contribution of the present research programme is that prefrontal cognitive control plays an essential role during the production of slow motor behaviours. Rather than a co-existence of two timing-processes, the present body of work supports an alternative view of motor timing insofar as the production of fast and slow movements relies on a similar motor mechanism. Cognitive monitoring would be additionally involved in the production of slow movements in order to slow the pace of motor execution. This view provides new insights into the cognitive and brain mechanisms underlying adaptative human behaviour.

Keywords: predictive timing; emergent timing; sensorimotor synchronisation; motor control; frontal activity; cerebral oximetry

GRAPHICAL ABSTRACT



RÉSUMÉ

Afin d'interagir avec leur environnement, les êtres humains adaptent en permanence la cadence spontanée de leurs actions. Les progrès de la recherche en psychologie du temps ont montré que deux processus (automatique et contrôlé) sont impliqués dans le traitement de l'information temporelle. Cependant, les mécanismes cognitifs et les régions cérébrales qui sous-tendent le contrôle temporel des comportements moteurs restent flous. L'objectif général de ma thèse est d'examiner les ressources cognitives et cérébrales nécessaires lors de l'exécution d'actions réalisées selon différentes contraintes temporelles. Dans la première étude, le contrôle cognitif appliqué lors du contrôle temporel des actions a été étudié à partir de l'analyse de séries temporelles et d'un paradigme de double tâche. Les résultats montrent que les mouvements rapides et lents impliquent des stratégies de chronométrie distinctes, caractérisées par des demandes attentionnelles hétérogènes. Dans la deuxième étude, la technique de neuroimagerie *f*NIRS a été utilisée pour examiner simultanément l'oxygénation des régions préfrontales et motrices pendant l'exécution de mouvements volontaires des membres supérieurs à différentes vitesses. Les résultats indiquent que les mouvements rapides impliquent une plus grande activité des régions motrices, tandis que les mouvements proches du rythme spontané exercent une plus grande charge sur le cortex préfrontal postérieur. La troisième étude a été conçue pour examiner la validité écologique des tâches de chronométrie motrice en fournissant une comparaison directe entre les tâches consistant à taper du doigt (finger tapping), à taper du pied et à marcher sur place. Les résultats montrent que les mouvements d'un seul membre et ceux du corps entier impliquent des stratégies de chronométrie motrice distinctes ; cela suggère que les paradigmes de tapping pourraient être trop éloignés des comportements naturels pour fournir des résultats généralisables. Par conséquent, dans la quatrième étude, la technique *f*NIRS a été utilisée pour examiner l'activité cérébrale préfrontale et motrice pendant l'exécution, à différentes vitesses, de mouvements des membres supérieurs mais également du corps entier. Les résultats indiquent que la production de mouvements lents entraîne une augmentation des activations préfrontales uniquement dans des tâches impliquant le corps entier. Il est à noter qu'une grande variabilité dans les réponses hémodynamiques des participants a été observée. Par conséquent, dans la cinquième étude, trois études de cas ont été menées pour évaluer la fiabilité test–retest des signaux hémodynamiques, et pour définir le nombre d'essais nécessaires pour des procédures block design dans le cadre de paradigmes moteurs menés en imagerie cérébrale *f*NIRS. La contribution originale de cette thèse porte sur le rôle essentiel que joue le contrôle cognitif préfrontal lors de la production de comportements moteurs lents. Plutôt qu'une coexistence de deux processus distincts, je soutiens une vision alternative de la chronométrie motrice dans la mesure où la production de mouvements rapides et lents repose sur le même mécanisme moteur. Le contrôle cognitif serait en outre impliqué dans la production de mouvements lents afin de ralentir le rythme de la production motrice. Cette vision ouvre de nouvelles perspectives sur les mécanismes cognitifs et céré-

braux qui sous-tendent l'adaptation du comportement humain aux contraintes de l'environnement.

Keywords: timing événementiel ; timing émergent ; synchronisation sensorimotrice ; contrôle moteur ; activité frontale ; oxymétrie cérébrale

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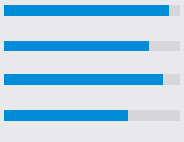

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ACRONYMS

AC	autocorrelation
ANOVA	analysis of variance
CPG	central pattern generator
DWA	detrend windowed autocorrelations
EEG	electroencephalography
*f*MRI	functional magnetic resonance imaging
*f*NIRS	functional near-infrared spectroscopy

HbO_2	oxygenated haemoglobin
HR	heart rate
HbT	total haemoglobin
HHb	deoxygenated haemoglobin
HRF	haemodynamic response function
IRI	inter-response interval
ISI	inter-stimuli interval
NHST	null-hypothesis significance testing
PSD	power-spectrum density
RM ANOVA	repeated-measures analysis of variance
RT	reaction time
SESOI	smallest effect size of interest
SMA	supplementary motor area
SMS	sensorimotor synchronisation
SMT	spontaneous motor tempo
SPA-*f*NIRS	systemic-physiology-augmented *f*NIRS
TOST	two one-sided tests

Part I

GENERAL INTRODUCTION

1 INTRODUCTION

1.1 THE MOST COST-EFFECTIVE BEHAVIOUR

Human beings are a product of natural selection. Natural selection favours characters that fit the individual best for life in its present environment by privileging sets of genes that minimise costs and/or maximise benefits. As with any other animal, costs usually refer to mortality and energy losses and benefits to fecundity and energy gains (Alexander, 1996). Energetics (i.e., the properties of an organism in terms of energy) is a concept of particular importance in moulding the evolutionary process, as acknowledged nearly a century ago by Lotka (1922).

Locomotion was likely important in the energy budget of early humans because of its fundamental role in food acquisition and survival. Thus, human evolution may have been strongly influenced by selection for structures and patterns of movements that reduce the energy cost of locomotion (Wells, 1988). In particular, Alexander (2002) stated that:

> Humans seem to adjust their walking and running gaits to minimise the metabolic energy cost of locomotion. The walking speed that we tend to prefer is the one that minimises energy cost per unit distance [...]. (p. 641)

Experimental evidence has shown that the energy cost per unit distance is minimal around 1.3 m/s (Bastien et al., 2005; Ralston, 1958; Zarrugh et al., 1974), which corresponds to two steps per second (i.e., 2 Hz). This particular frequency is the natural and confortable walking pace of humans, referred to as the spontaneous motor tempo (Fraisse, 1982; MacDougall & Moore, 2005; Moelants, 2002). Of interest, energy cost was also found to shape the characteristics of upper-limb movements (e.g., arm reaching; Nishii & Taniai, 2009; Shadmehr et al., 2016; Taniai & Nishii, 2015), which are also spontaneously produced at ~2 Hz (Rose et al., 2020).

The "most cost-effective behaviour" changes according to environmental constraints. As an example, individuals transition to running when the walking speed becomes too high in terms of energy expenditure (Alexander, 1996; Brill & Kram, 2021; Srinivasan & Ruina, 2006). Such a behavioural transfer occurs around 2 m/s (i.e., 3.1 Hz; Rotstein et al., 2005) and serves to minimise the energetic cost of locomotion. Thus, minimising the energy cost of a particular behaviour (e.g., bipedal locomotion) does not consist of performing a pattern of movement that is strictly determined by evolution. Rather, energetic cost minimisation relies on the ability to adapt the pattern of movement to present constraints.

The ability to perform the most cost-effective behaviour is improved through experience. Ivanenko et al. (2007) showed that toddlers learn to achieve an optimal locomotor pattern for walking as part of their development. Through trial and error, individuals progressively embrace energy-saving behaviours (Alexander, 2002). The metabolic cost of new movements (i.e., arm reaching and walking) was indeed

found to reduce on the same timeline as improvement in motor learning (Finley et al., 2013; Huang et al., 2012). In addition, experimental evidence has indicated that, when exposed to perturbations, individuals modified the pace of their behaviours to converge on new energetic optima within seconds (Sánchez et al., 2017; Selinger et al., 2015).

An implication of the energetic cost-minimisation framework entails that energy cost is not just the outcome of motor production, but continuously shapes the movements that are performed (Cheval et al., 2018a). Individuals pursue a good balance between energy cost and reward – this is the basic definition of efficiency. Thus, most animals spend a negligible part of their time moving at maximal and minimal speed because it entails a metabolic cost that is excessively high when compared to the reward of the action (e.g., travelling between two locations; Alexander, 2003; Berret & Jean, 2016). Nonetheless, some rewards can make it worthwhile to perform movements that are energetically inefficient (Shadmehr et al., 2016; Summerside et al., 2018). This is, for example, the case when time is valuable (e.g., not missing a train) or accuracy is of particular importance (e.g., avoiding water puddles).

Aside from metabolic cost, producing energetically inefficient behaviours requires cognitive resources. Using an approach–avoidance task, Cheval et al. (2018b) found that avoiding sedentary behaviours elicited larger fronto-central N2 event-related potential than avoiding physical-activity behaviours. Interestingly, the N2 amplitude was found to reflect inhibition of automatic motor responses (for a review, see Folstein & Van Petten, 2008). Taken collectively, these findings suggest that a high level of cognitive control is required to counteract a general tendency to perform energy-saving behaviours (Cheval & Boisgontier, 2021; Cheval et al., 2020).

1.2 A TWO-SYSTEM APPROACH OF COGNITION

Individuals are automatically attracted towards behaviours that minimise energetic cost. Nonetheless, energetically inefficient behaviours can be performed at a significant cognitive cost if the associated rewards are sufficient. Research at the cornerstone of decision making and motor control found that individuals can indeed decide to perform a metabolically expensive action if its expected utility (i.e., subjective valuation) was rated as high (Codol et al., 2020; Rigoux & Guigon, 2012). This suggests that motor control reflects the brain's economic evaluation of an action outcome (Shadmehr et al., 2019).

A behaviour is not solely the outcome of an action realisation; it also refers to a decision, which is the result of a balance between costs and benefits of plausible actions. This process requires prediction. To make the choice of preforming energetically inefficient behaviours, individuals need to "look into the future" and predict the impact that an action will have on the body and environment (Bubic et al., 2010). Thus, human beings possess the means to counteract their inclination of executing instinctive behaviours.

Over the last three decades, psychologists have suggested that the human mind is composed of two modes of thinking (i.e., dual-system framework; see e.g., Diederich & Trueblood, 2018; Epstein, 1994; Frankish, 2010; Stanovich & West, 2000). Those two systems, widely known as System 1 and System 2, govern the way individuals think

and behave. System 1 is described as automatic and effortless. System 2 is effortful and associated with enhanced monitoring. Depending on the individual's resources and external constraints, one system will influence behaviour to a greater degree than the other (Kahneman & Frederick, 2002).

System 1 proceeds fast and in an automatic way (i.e., with no effort). In addition, System 1 cannot be shut down *ad libitum* (Sloman, 1996). This mode of thinking operates with no sense of voluntary control, leading it to be considered the most primitive system (Frankish, 2010). As an example, individuals make use of System 1 when they complete the sentence "You can't judge a book by its ..." (or "Il ne faut pas juger un livre à sa ..." for the French readers). Most of the time, individuals rely on System 1 to think and behave because it is fast and requires less cognitive resources than System 2 (Kahneman, 2011).

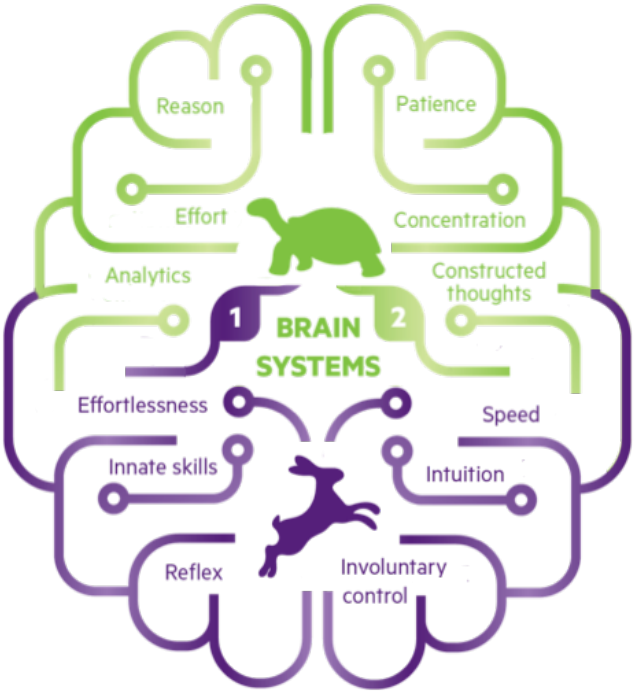
System 1 is in charge of making routine decisions and performing usual behaviours. Because they are governed by habit, the operations of System 1 are hardly controllable (Kahneman, 2003). Thus, the instinctive tendency of an individual to perform energy-saving behaviours would be the cause of System 1 cognitive operations. System 1 has been shaped by evolution to gauge constantly and without effort how things are going (Kahneman, 2011). Occasionally, individuals face situations for which System 1 is useless or insufficient (e.g., remember the last time you saw a specific person). In such particular situations, System 2 takes over and control the impulses of System 1 (Alter et al., 2007).

System 2 operates slowly and is quite flexible. Moreover, System 2 exerts voluntary attention when needed and applies a deliberate control over behaviour, leading it to be considered as specific to humans and phylogenetically young (Evans, 2003). Nonetheless, this system has a limited processing capacity and requires substantial mental effort. Because the operations of System 2 are demanding in terms of cognitive resources, the efforts invested (i.e., focus on the task and intentional monitoring of attention) never exceed what is strictly necessary (Kahneman, 2011).

System 2 has the faculty to modify the operations of System 1 by monitoring the normally automatic function of attention. The mobilisation of System 2 allows to override the routine, "mindless" behaviours. Because the instinctive and effortless System 1 is usually very efficient to deal with ordinary situations, the deliberate and costly operations of System 2 are used only when the individuals encounter complex and critical situations. Thus, the division of tasks between System 1 and System 2 is highly efficient in the sense that it minimises cost and maximises performance (Kahneman, 2011).

A limitation in the alternation of System 1 and System 2 operations is time pressure. Empirical findings showed that errors pertaining to the activity of System 1 are not corrected when individual have only little time to answer (Finucane et al., 2000; Maule & Svenson, 1993). The operations of System 2 take time to be implemented (Kahneman, 2003). This implies that System 2 is less likely to be effectively mobilised when the situation requires fast reactions. Therefore, fast actions would emanate from System 1 activities whereas slow actions would depend on the level of attentional and inhibitory control that is set upon System 1 by System 2 operations.

Figure 1
Illustrations of the Dual-System Framework



Note. Image sourced from PNGitem.

1.3 EMERGENT AND PREDICTIVE TIMING

Some actions are highly efficient when performed quickly and without even thinking about the executed movements (e.g., to whip up egg whites by hand). In this instance, System 1 alone is sufficient to take charge of action execution. In contrast, there are actions for which slow movements are particularly effective (e.g., to insert a thread through the eye of the needle). In such cases, the mobilisation of System 2 is beneficial, even though it entails significant cognitive effort.

In the scientific literature pertaining to the psychology of time, the way movements are temporally controlled was examined by two intellectual traditions (i.e., dynamical systems vs. cognitive framework). The dynamical systems framework posits that temporal regularities of movements implicitly emerge from the kinematic parameters of effectors (e.g., hand, forearm, leg), considered as self-sustained oscillators (Lemoine & Delignières, 2009). More precisely, Repp and Steinman (2010) stated that such emergent timing "arises from the dynamic control of nontemporal movement parameters such as stiffness" (p. 11). Thus, emergent timing is generated solely by movement dynamics, without the need to internally control the timing of movements (Torre et al., 2010).

The cognitive framework proposes, in contrast, that movement timing originates from an explicit, cognitive representation of time. Movements are triggered by a kind

of "internal clock" that provides a sequence of periodic timing events (Delignieres & Torre, 2011). Such predictive timing (or event-based timing) involves a representation of time that is abstract and independent of the effector(s) involved in the motor action. Thus, emergent and predictive timing belong to two opposite and concurrent theories (dynamical vs. cognitive) in the sense that they predicate motor timing as being implicit vs. explicit, respectively.

With the intent of conciliating these two parts of the scientific literature, researchers have shown that emergent and predictive timing were specific to two different types of motor tasks. Due to their dynamic nature, continuous movements (e.g., circle drawing) were found to make use of emergent timing while discrete movements (e.g., finger tapping) called on predictive timing (Robertson et al., 1999; Studenka and Zelaznik, 2008; Zelaznik et al., 2000, 2005, 2002). Such task-related dichotomy was further supported by the findings that patients with cerebellar lesions were impaired during the production of discrete but not continuous movements (Spencer & Ivry, 2005; Spencer et al., 2003).

The apparent division between emergent and predictive timing to control motor performance as a function of task parameters is, nonetheless, less unequivocal during ambivalent motor tasks. The air-tapping task is a finger-tapping task that occurs in the air (i.e., without contact on a surface). Spencer et al. (2003) showed that such an ambiguous task can be executed using emergent timing when the participants were instructed to perform smooth movements, and using predictive timing when instructed to pause briefly between each movement. Notably, the air-tapping task was found to elicit one or the other timing depending on participants when no specific performance instructions were given (Delignieres & Torre, 2011).

Instead of representing a similar process within two irreconcilable theoretical frameworks, emergent and predictive timing would reflect two different *modes* of motor control (automatic vs. cognitive). Similarly to the engagement of System 1 and System 2, these two timing modes could be implemented depending on the individual's resources and task constraints. This notion is further corroborated by the finding that movement rate is also a key task parameter that determines the timing strategy used. More precisely, fast-rate movements depend upon emergent timing while slow-rate movements rely on predictive timing (see Dione & Delevoye-Turrell, 2015; Huys et al., 2008; Maes et al., 2015).

Experimental evidence has shown that emergent timing is specific to movements performed with the dominant hand (Studenka & Zelaznik, 2008). In addition, Summers et al. (2010) found that older participants were significantly impaired in motor tasks requiring predictive timing but matched younger adults' performance in motor tasks demanding emergent timing. This indicates that an age-related decline in cognitive performances does not affect emergent timing process. Collectively, these results suggest that emergent timing is observed more specifically in highly-automated movements that do not require – or little – cognitive control, which are peculiar to System 1 activity. In other words, emergent timing would be the timing mode used when individuals perform actions using System 1.

Additional findings suggest a relationship between cognitive functioning and predictive timing abilities. Baer et al. (2013) showed that musical training impacted temporal variability in motor task requiring predictive but not emergent timing. No-

tably, experimental evidence has confirmed that musical training is associated with cognitive benefits both in young and older adults (Amer et al., 2013; Bialystok & DePape, 2009; Strong & Mast, 2018). It is therefore possible that predictive timing is implemented for actions performed under the cognitive wings of System 2.

Using dual-task paradigms, attentional demand was indeed found to be higher during the production of discrete but not continuous movements (Maes et al., 2015; Summers et al., 2008). In addition, Krampe et al. (2010) showed that dual-task cost during a finger-tapping task were more pronounced at slower tempo when compared to close-to-spontaneous pace; nonetheless, a fast-tempo condition was not included in the experimental paradigm. Thus, attention process, which is distinctive feature of System 2 functioning, could be a key component of predictive timing.

A distinctive feature of System 1 and System 2 is their temporality: While fast actions would emanate from System 1 operations, slow actions would depend on System 2 functioning. Thus, emergent timing, characteristic of fast movements, would be an automatic process (i.e., System 1 operations); predictive timing, characteristic of slow movements, would involve a high-level representation of time (i.e., System 2 operations) that is directly dependent on cognitive functioning. The general aim of my thesis was to test the hypothesis that cognitive control is applied when performing slow-pace movements and automatic control is implemented when executing fast-pace movements.

1.4 BRAIN CORRELATES

If emergent and predictive timing refer to two different modes of motor control (automatic vs. controlled), they should involve two different pattern of neural activation. More precisely, emergent timing should be underpinned by cerebral structures that are characteristic of automatic, non-controlled processes (e.g., basal ganglia, motor areas; Saling & Phillips, 2007; Sumner & Husain, 2007). By contrast, predictive timing should involve brain areas representative of effortful, high-level cognitive processes (e.g., prefrontal cortex; Frith & Dolan, 1996; Koechlin et al., 2003; Miller & Cohen, 2001).

Supporting this notion, neuroimaging studies highlighted a duality of neural system for time measurement. A couple of meta-analysis reported that motor tasks associated with emergent timing activate mainly the motor system (e.g., supplementary motor area, sensorimotor cortex, basal ganglia) while those associated with predictive timing activate predominantly the frontal and parietal cortex (e.g., dorsolateral and ventrolateral prefrontal cortex, inferior parietal cortex; Lewis and Miall, 2003a, 2003b). Wiener et al. (2010b) meta-analysis also found that sub-second timing tasks involved mostly sub-cortical areas (e.g., basal ganglia) and supra-second timing tasks recruited cortical structures (e.g., prefrontal cortex, supplementary motor area; see also Lewis & Miall, 2003c). Moreover, implicit-timing tasks were found to activate the left premotor and parietal cortices and explicit-timing tasks the basal ganglia, supplementary motor area, cerebellum, and prefrontal cortex (Coull & Nobre, 2008; Coull et al., 2011; Wiener et al., 2010a). Taken collectively, these findings support the hypothesis of a dual-mode model for timing.

While the brain regions that are relevant to interval timing are still debated (Nani et al., 2019), distinct neural structures seem to support emergent and predictive timing. It is noteworthy, however, that neuroimaging studies examining the brain correlates of predictive timing used perceptual tasks (e.g., time estimation, time discrimination) while those investigating the neural substrate of emergent timing used motor tasks. Thus, in meta-analyses comparing the brain areas involved in emergent vs. predictive timing, findings can be confounded by task characteristics. In addition, the neuroimaging studies using motor tasks employed minimalist movements (e.g., finger tapping, pressing a button) that are quite different from everyday-life body movements (e.g., walking).

A limitation of the current neuroimaging techniques (e.g., functional magnetic resonance imaging [*f*MRI], electroencephalography [EEG]) is their sensitivity to movement artefacts, making it difficult to monitor brain activation during ecological motor production. Over the last decade, the optical technique of the functional near-infrared spectroscopy (*f*NIRS) has become the reference tool for neuroscientists investigating brain activation using motor paradigms. Discovered in the late 70's (Jöbsis, 1977), this non-invasive technique benefits from several advantages: low acquisition costs, continuous long-time monitoring, short installation time, portability, and robustness to motion artefacts (Leff et al., 2011).

Making use of infrared light (i.e., wavelengths of 700–900 nm), *f*NIRS monitors the relative changes in oxygenated (HbO_2) and deoxygenated (HHb) haemoglobin concentrations in cortical grey matter (recording depth of ~5–8 mm; Huppert, 2016). The local haemodynamic response refers to the increase in cerebral blood flow observed following neuronal activity in order to meet the energy needs (i.e., oxygen, glucose) of the active cells (Magistretti et al., 1999). Such neurovascular coupling results in an increase in HbO_2 and a decrease in HHb concentrations that allow researchers to infer cortical activation. Thus, the *f*NIRS technique can be used to examine the involvement of different brain activation patterns as a function of task demands (i.e., implementation of emergent vs. predictive timing) during motor paradigms.

1.5 THE PRESENT PROGRAMME OF RESEARCH

The general aim of my thesis was to examine the cognitive and cerebral resources needed during the execution of voluntary actions performed under different time constraints. More precisely, both behavioural indices and neuroimaging evidence were used to test the hypothesis that slow-paced movements are underpinned by prefrontal cognitive control while fast-paced movements are supported by motor automatic control. In Chapter 2, the methodological details pertaining to the present programme of research are detailed. Chapters 3–7 constitute the experimental and theoretical contributions, whose aim was to enhance knowledge regarding the cognitive and brain mechanisms involved in the timing of motor behaviours.

In Chapter 3, the involvement of cognitive control in motor timing was investigated using time series analysis and a dual-task paradigm. In Chapter 4, the *f*NIRS neuroimaging technique was used to examine the cerebral oxygenation of prefrontal and motor areas simultaneously during the execution of upper-limb motor tasks

performed under different time constraint. Chapter 5 presented a study that was designed to investigate the ecological validity of motor-timing tasks by providing a direct comparison across the tasks of finger tapping, foot tapping, and stepping on the spot.

In Chapter 6, the *f*NIRS technique was employed to examine prefrontal and motor activation during the execution of upper-limb and whole-body movements under distinct time constraints. In Chapter 7, three case studies were conducted to assess the test–retest reliability and define the appropriate number of trials necessary for a block design procedure in *f*NIRS brain imaging during motor paradigms. Finally, Chapter 8 presents a general discussion of the experimental findings obtained in the course of this 3-year programme of research.

Part II

METHODS

2

METHODOLOGICAL CONSIDERATIONS

2.1 DIGITAL REVOLUTION OF HUMAN SCIENCES

The ability to collect a large amount of human-generated data represents an incredible opportunity for scientists in the field of psychology. Accurate measurement facilitates a broader understanding of the cognitive processes under investigation. Digital technologies have lead to significant advances in research through offering new tools, increasing the frequency of data acquisition, and enabling the automation of both data collection and analyses.

As a young researcher in psychology, dealing with a gargantuan volume of data can be disconcerting. I remember the first time I opened a participant data file containing half-a-million rows and a few dozen columns. I did not even know where to start in terms of computing the variables of interest! Over the course of my PhD, I had to learn about good practices and the appropriate tools that could be applied to the data I was collecting. In this section, I report the choices I made in optimising the management of large data sets.

2.1.1 *Automation of Markers*

When several measuring tools are used in tandem, it is important to be able to synchronise the epochs that they capture. I wanted to record brain activity while my participants were moving at different frequencies. Therefore, a crucial point was to know exactly when a participant initiated and ended a movement. Several possibilities are available to the experimenter: The first one is to write down the precise time for each start and end of a series of movements. This way of proceeding is quite challenging for the experimenter, limited in terms of time precision, and prone to recording errors.

The second possibility is to manually add a marker during the experimental session on the different acquisition systems at the beginning and end of each trial. Again, this requires relentless concentration (if a marker is missed, it will be lost) and is not very accurate (a delay of a few seconds is likely to occur); besides, manual marking may be impossible to implement when the computers directing the data acquisition are located far apart. A third possibility is to automate the marker sending. Practically, this implies that the master computer (i.e., the compute that is managing the presentation of the different experimental conditions) is connected to all other computers (e.g., via a parallel port). Automation of the initiation of markers allows the researcher to know *exactly* when a trial starts and ends (i.e., precision of the millisecond order), and to have perfect synchronisation between the different acquisition systems, regardless of their number. In addition, it frees the experimenter to focus on the participant's behaviour.

Implementing the automation of markers requires rigour and deep thoughts. First and foremost, the values sent to the different acquisition systems need to be defined. At this point, the researcher must already have in mind how they will preprocess and analyse their data. All the studies of my PhD programme used a block-design procedure; hence, the trials running consecutively were eventually averaged. Thus, specific marker values were defined for each experimental condition. For example, the value "3" corresponded to the beginning of a fast trial, while a "4" corresponded to the beginning of a slow trial. Accordingly, errors in trial labelling were avoided, and the trials corresponding to the various experimental conditions were easily averaged. It is worth noting that sending the same values to the various acquisition systems allows for consistency, and reduces the time taken to develop data-processing algorithms (see Subsection 2.1.3).

The period of time during which a marker is sent represents also a salient consideration. This depends on the sampling frequency of the data acquisition (i.e., the number of samples obtained in 1 s). Moreover, if the period of time during which a marker is sent is less than the period between two measurement points, the marker might be missed. Thus, if the sampling frequency of *f*NIRS recordings is 4Hz (i.e., four measurements per second), markers need to be sent for more than 250 ms. Given that the same markers were sent to all three data acquisition systems, I used the system with the lowest sampling frequency (i.e., *f*NIRS) to define the period of time during which the markers were sent.

2.1.2 *Data Management*

Data are the most precious thing a researcher possesses – that is what leads Strevens (2020) to state that scientists have a "life consisting almost entirely of the production of experimental data" (p. 34). Data allow the researcher to (dis)confirm research hypotheses, generate scientific knowledge, and ultimately lead to advances in conceptualisation. Therefore, it is essential to understand the importance of redundant data storage. I have made a habit of *always* storing the (properly marked) data in several different locations (i.e., internal and external hard drives, personal institutional cloud, laboratory cloud). This way of proceeding prevents the loss of data – and of time and money since extra hours of data collection will not be necessary!

Both the raw acquisition files and the ensuing readable exports need to be stored. Keeping the raw acquisition files is always a good idea, because it allows the researcher to redo as many exports as necessary (e.g., in case they forget to include the headers). In addition, the raw acquisition files contain valuable information, such as the sampling frequency and automatically applied filters. The readable exports (e.g., with .txt, .xlsx, .tsv file extensions) are essential because these data files are easily read by common computer software. Thus, they are the files that are used by researchers to perform data analysis. Note that exporting the recordings into readable files and saving both the exports and acquisition files should be done after *each* experimental session (or each day of data collection), especially if the equipment is shared between different researchers.

Experimenters are well advised to properly organise their data for the reason that it optimises its discovery and improves research transparency. This is especially

true when dealing with a large volume of data. For example, I never mix raw and preprocessed data, and thus store them in different folders. In addition, I opt for meaningful names for my files (e.g., containing project acronym, date, version number). Finally, I separate in-progress and complete work, and add .txt files in each of my folders to describe its contents and provide significant information (e.g., if the figures plotted are outliers free, how an outlier was identified, the parameters of the statistical test used). Best practices and guidelines for a good data-management routine are readily available on numerous data science websites (e.g., R-bloggers); in addition, tools can be used to assist and facilitate the organisation of data (e.g., folder structure generator; De Kok, 2018).

2.1.3 *Data Processing Algorithms*

Some data sets are easily analysed – think of a single questionnaire filled out by patients and a control group. However, when working with sizeable files (as is the case with brain imaging), data analysis can quickly become extremely onerous. In this case, researchers have to leave the traditional approach (e.g., using Excel), and take advantage of data science tools that enable the manipulation and arrangement of such substantive file.

Unfortunately, I did not have the chance to take algorithm and code courses during my previous psychology degrees. Thus, one of the first things I did as a PhD student was to learn the programing language R (through DataCamp courses) and read the outstanding text *Comprendre et réaliser les tests statistiques à l'aide de R* (Millot, 2011). I chose R because this language benefits from a large collection of statistical libraries and produces powerful and appealing graphs (see e.g., R Graph Gallery; Holtz, 2018). Accordingly, I use the single software to handle data preprocessing, statistical analyses (see Section 2.2), and data visualisation.

The processing of data using computer algorithms (i.e., bounded and unambiguous sequences of instructions) is powerful because a series of complex operations is automatically performed on each file contained in a folder, without the need to open the files one by one. In addition, the value of a parameter can be easily modified by amending the corresponding line of code, without having to redo the series of calculations in each data file. Importantly, the researcher keeps a record of every computation and transformation performed on the data – the sequence of lines of code is actually an exhaustive history.

Using computer algorithms also allows the researcher to readily share the data analysis pipeline with collaborators along with the scientific community, which serves to improve research transparency. To this end, the use of R notebooks is advantageous given that it provides the means to intersperse segments of code with narrative descriptions (e.g., description of the rationale behind the conducted analyses). Each segment of code can be executed individually, with the output (e.g., data visualisation) visible immediately beneath the corresponding lines of code.

The development of a computer algorithm to process data takes significant amounts of time. Several days or weeks of design and writing are required, and numerous lines of code will be altered or removed during the process. In order to keep track of all the changes that have been made, the use of a version control system is recom-

mended. I decided to use Git because my university has a GitLab server. The scripts contained in a predefined GitLab repository on the researcher's computer are sent to a GitLab server. Ideally, this synchronisation should be done at the end of each processing step development. A version is created for each upload on the server and different versions can be compared to track each character that is either added or deleted. Using GitLab also enables the researcher to have a backup of the data analysis algorithms in case the local files (i.e., on the researcher's computer) are corrupted. GitLab projects can be made public in order to share computer algorithms pertaining to a research project; for example, in the context of a scientific publication to adhere to the Open Science principles.

2.2 STATISTICAL APPROACH

For the uninitiated reader, the link between psychology and statistics may seem surprising. I remember my family being quite astonished about the number of statistical courses I followed as an undergraduate student. Yet statistical literacy is a significant component of psychological sciences, and thus mastering a variety of statistical tools was an important skill for me to acquire.

At the advanced stages of a research project, the implementation of statistical procedures is a convention that serves to highlight significant differences among groups. Although less common, a category of statistical tests is specifically designed to verify an absence of difference. Statistics are also essential at the beginning of a research project when estimating the number of participants to be recruited. The aim of this section is to provide insight into the statistical procedures that I adopted in the experimental studies of my thesis.

2.2.1 *Sample Size Computation*

In the early stages of a research project, a scientist need to consider a crucial question: How many participants do we need to recruit? For a long time, researchers largely employed rules of thumb to define the participant sample size (e.g., at least 20 observations per cell of statistical analysis; Simmons et al., 2011). About 12 years ago, only ~10% of a selection of human sciences articles published since 2000 included a sample size justification (Aguinis & Harden, 2009).

Justification of the participant sample size is an important consideration that needs to be carefully addressed, especially at a time when the scientific community is increasingly concerned about the reproducibility of experimental results (see e.g., Baker, 2016; Fanelli, 2018; Pashler & Wagenmakers, 2012). Notably, sample sizes that are too small lead to low statistical power and inconsistent statistical inferences, with significance levels that "can change dramatically as additional observations are added or from one study to the next" (Lakens & Evers, 2014, p. 280). For this reason, it is increasingly difficult to publish a study that does not include a sample size justification and/or estimation.

Defining an adequate sample size also has ethical implications. A study with an insufficient sample size is uninformative; thus, participants who volunteered wasted their time, which is arguably unethical (Lenth, 2001). Conversely, a study with an

excessively high number of participants is overpowered, which means that human and others resources were wasted. Again, this is arguably non ethical.

There exists several approaches that can be applied to justify a sample size (e.g., measure of the entire population, resources constraints; Lakens, 2021a). I decided to rely on statistical power, namely the probability of detecting an effect (i.e., non accepting the null hypothesis) provided that this effect exists. An a priori power analysis aims to estimate the required sample size to detect an effect of a given magnitude, with the desired statistical power. To execute such an analysis, three parameters must be provided: the alpha level, power, and effect size.

In the experimental studies of the present programme of work, the alpha level was set at .05 (i.e., probability of 5% to erroneously not accept the null hypothesis in the long run; Type I error), which is the gold standard in the field of psychology. Power was fixed at .8 (i.e., probability of 80% to accurately reject the null hypothesis in the long run), which corresponds to a β level of .20 (Type II error). I made this choice in a way that the Type I error is four times less likely to occur than the Type II error (Cohen, 1988).

The expected effect size was estimated from previous similar studies in terms of variables of interest and experimental design. The a priori power analyses were computed using the G*Power software (v.3.1.9.4; Faul et al., 2007). A few additional participants were recruited in each study to account for missing data and outliers, which are common in experimental work (for reviews, see Aguinis et al., 2013; Graham et al., 2012). In addition, all the studies reported in the present thesis were submitted for ethical approval before their initiation (see Appendix A).

2.2.2 *Null-Hypothesis Significance Testing*

The null-hypothesis significance testing (NHST) is the most widely used statistical approach to test research hypothesis in psychology. In this framework, two hypothesis are defined: the null hypothesis (i.e., H_0; no differences between groups) and the alternative hypothesis (i.e., H_1; directional or non directional differences between groups). The p value indicates whether the value of a statistical test (e.g., t, F) is consistent with the probability distribution under H_0, which is the default explanation. If the p value is $< \alpha$, H_0 is rejected; otherwise, H_0 can not be rejected.

For several decades, the use of NHST and the associated p value have been criticised by some researchers, and alternative statistical approaches have been suggested (e.g., Bayesian inference; Dienes & Mclatchie, 2018; Kelter, 2020; Wagenmakers, 2007). The limitations pertaining to the NHST have to do with (a) concluding a meaningful effect is absent after a non-significant result, or (b) misinterpreting a significant result as an important effect (Kline, 2013). Thus, the problem associated with the NHST is related to exaggerated interpretation of what can be inferred from the outcome of a statistical test. Accordingly, Lakens (2021b) stated that:

> In certain situations, such as well-controlled experiments where we want to test ordinal claims, p values can provide an answer to a question of interest. Whenever this is the case, we do not need alternatives to p values – we need correctly used p values. (p. 7)

In the experimental studies of my thesis, the NHST was used only to test predefined research hypothese involving an expected difference among experimental groups. For each operational hypotheses, the critical statistical test (e.g., omnibus test, post hoc test) was clearly indicated. Careful caution was taken with regard to the assumptions underlying the application of each statistical procedure (e.g., normality, homoscedasticity). Appropriate correction for multiple comparisons was applied when necessary. In addition, the p values were interpreted in a measured, considered manner by considering effect sizes (see Subsection 2.2.3).

2.2.3 *Smallest Effect Size of Interest*

A p value does not allow the researcher to quantify statistical evidence; namely, there is no linear relationship between the p value and the effect size. In addition, a significant statistical test (p value $< \alpha$) does not provide an unequivocal proof that a true effect exists. Because inferential statistics are based on probabilities, there is a likelihood of making an incorrect conclusion when rejecting the null hypothesis (i.e., false positive). This is what led Gene V. Glass (1997), a renowned statistician, to say:

> Statistical significance is the least interesting thing about the results. You should describe the results in terms of measures of magnitude – not just, does a treatment affect people, but how *much* does it affect them. (as cited in Hunt, 1997, p. 29)

The effect size provides a quantification of an experimental-effect magnitude (Sullivan & Feinn, 2012). Consequently, I systematically reported the effects size pertaining to each statistical test (e.g., Cohen's d, η_p^2) in the experimental studies of this thesis.

The effect size can help a researcher determine whether the observed significant p value is informative. Think of an experiment reporting a significant effect ($p < .05$) for eating soup at dinner on an individual's height. We can easily imagine that the researcher is pleased that the efforts invested in the study are rewarded. If one were now to assume that the observed difference between the two experimental groups (i.e., soup eaters vs. non soup eaters) is 5 mm, which corresponds to a very small effect size. We could ask the following question: Is it reasonable to conclude that eating soup makes you grow? The researcher will likely seek to replicate their results by increasing the statistical power (e.g., by including more participants).

The challenge is to determine which effect size is sufficiently large to be informative. The difference between the experimental groups that is considered big enough to be meaningful is referred to as the *smallest effect size of interest* (SESOI; Lakens, 2014). Several approaches can be used to define the SESOI (e.g., use of benchmark, resource limitations; for a review, see Lakens et al., 2018). I decided to rely on the small telescopes approach (Simonsohn, 2015); accordingly, the SESOI was set to the effect size that an earlier similar study would have had 33% power to detect. For each research hypothesis of the present thesis, the SESOI was calculated using G*Power (v.3.1.9.4; Faul et al., 2007) and compared to the effect sizes obtained from the statistical tests.

2.2.4 *Difference and Absence of Difference*

The NHST does not enable the researcher to verify an absence of difference among experimental groups – absence of evidence is not evidence of absence. When the p value of a statistical test is larger than α, the only conclusion that can be drawn is that the observed data are not surprising under H_0 (Lakens, 2017). To endorse the null hypothesis, another statistical approach needs to be considered.

Equivalence tests provide the means to assess the similarity among experimental groups (Meyners, 2012). In particular, equivalence tests are designed to establish whether an effect is sufficiently close to zero to reject the presence of a meaningful difference. In equivalence testing, H_0 corresponds to the hypothesis that a meaningful effect exists in the population. If the statistical test is significant, H_0 is rejected.

A common approach of equivalence testing is the two one-sided tests (TOST) procedure (Schuirmann, 1987). In the TOST procedure, the SESOI is used to defined the difference that is too small to be meaningful. Accordingly, if the SESOI is set to d = .2, the lower equivalence bound (i.e., Δ_L) is equal to -.2, and the upper equivalence bound (i.e., Δ_U) to .2. The TOST examines whether the observed effect is smaller than Δ_L and larger than Δ_U. If the results of both t tests are significant, H_0 is rejected and the researcher can conclude that there is no significant difference between the two experimental groups under investigation (Lakens, 2017).

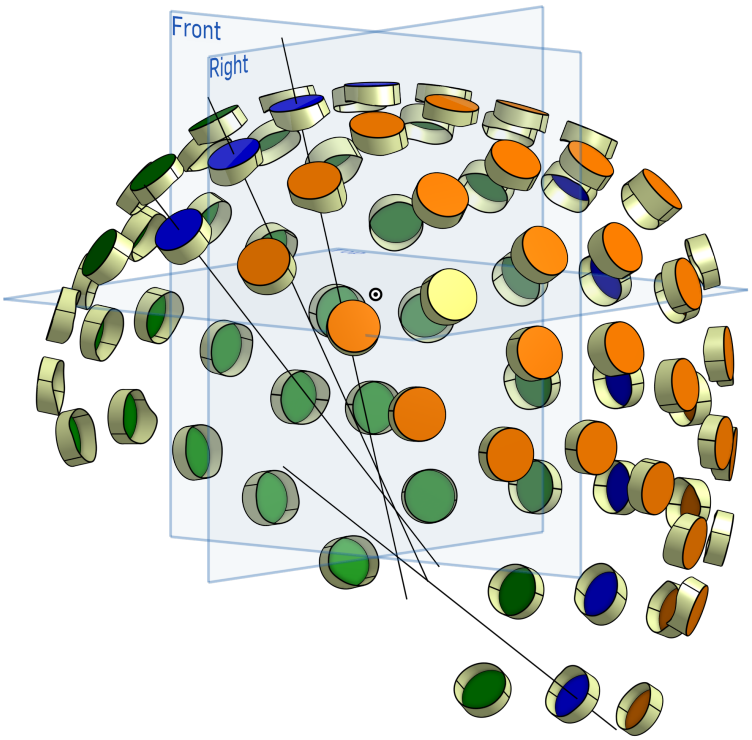
In the experimental studies of the present thesis, the TOST procedure was used to test research hypotheses involving an expected absence of difference among experimental groups. The SESOI was determined using the small telescopes approach, as described in Subsection 2.2.3. The TOSTs were computed using the TOSTER R package (Lakens et al., 2018).

2.3 DEVELOPMENT OF THE *f*NIRS TECHNIQUE

When I take a plane or a train, I like to buy a magazine at the newspaper kiosk. Every time I see a popular neuroscience periodical, I flick through it to see whether there is a mention of the *f*NIRS technique. I have not found this technique mentioned anywhere not even once. The *f*NIRS technique is indeed relatively recent when compared to other brain-imaging methods (e.g., EEG, *f*MRI). Notably, the Society for Near-Infrared Spectroscopy was created in October 2014. It it worth noting that the last decade has seen a lack of consensus regarding how to collect and process *f*NIRS data (see Herold et al., 2017; Menant et al., 2020). This is probably why *f*NIRS is not, as yet, a commonly used technique in the field of cognitive neuroscience. When I started my PhD in 2018, my research unit's lab already owned an *f*NIRS system (see Figure 2), but it had been underused for several years.

Before conducting in vivo brain recordings, the first step was to confirm that the *f*NIRS system was functioning correctly. To this end, phantom tests were executed. A phantom is an object specially designed to be a stand-in for human tissues. Such a device provides the researchers with the ability to examine the performance of imaging apparatus. The 32 optodes of the *f*NIRS system (FOIRE-3000/16; Shimadzu, Kyoto, Japan) were wired to two phantom devices provided by the manufacturer. Because the phantom simulated a homogeneous opaque environment, it was expected

Figure 2
3D Modelling of the fNIRS Headset



Note. Each disc represents an optode hole. Median optodes are coloured in blue, left-side optodes in orange, and right-side optodes in green. This 3D scan was performed at the Pôle AIP-PRIMECA (Valenciennes, France), with the gracious help of Jean-Dominique Guérin and Yann Konate.

that the amount of detected infrared light was *exactly* equal to the amount of emitted light. This prediction was supported for each pair of optodes, which served to confirm that the *f*NIRS system was operating satisfactorily.

Executing an *f*NIRS study is a challenging endeavour given the dearth of precise guidelines in the scientific literature. Several methodological choices were made to develop the research protocols of the *f*NIRS studies pertaining to the present programme of research. The main aim of this section is to explain and justify my choices.

2.3.1 *Dealing with Human Hair in Optical Imaging*

*f*NIRS is an optical imaging technique that makes use of the proprieties of light to identify cerebral activity. The basic principle is that infrared light is sent to the cerebral cortex and absorbed differently depending on local blood oxygenation. A salient issue is that hair is also an absorber of light. Koizumi et al. (1999) found

that hair follicles reduced infrared-light intensity up to 50%, especially in dark hair. In addition, hair can reduce the optical contact between the optode and scalp, and ultimately jeopardise *f*NIRS signals (Khan et al., 2012; Pollonini et al., 2016).

In a pilot study, we asked one participant with hair and one participant with a shaven head to perform a finger-tapping task in synchronisation with an auditory metronome at an interstimuli interval of 500 ms. The presence of hair drastically reduced the quality of the *f*NIRS recordings (see Figure 3). Thus, I took the decision to include only male participants with very short hair (< 1 cm) or shaven heads in the first *f*NIRS study of the present programme of work (see Chapter 4). This facilitated minimisation of the degree to which light was obstructed by the presence of hair. In addition, motion artefacts pertaining to the sudden loss of optical coupling between optodes and the scalp that were caused by hair (i.e., high-frequency spikes and baseline shifts) were duly avoided.

In term of generalising the results, it is, of course, problematic to derive conclusions solely from male and hairless participants. It was thus necessary to address the limitation pertaining to hair in *f*NIRS technology. In a fist step, the *f*NIRS headset must be fitted snugly to the participant's scalp to ensure proper optical coupling. Before each *f*NIRS recording, the nuts holding the *f*NIRS headset armature were loosened slightly so the experimenter could adjust the headset to the precise shape of the participant's cranium. Thereafter, the nuts were tightened in such a way that the gap between each optode hole and the participant's scalp was minimised.

This headset-fitting operation was difficult to execute on participants with a small head considering that we had only a standard-size headset. The *f*NIRS signal quality of these few participants was generally poor due to incessant losses of optical coupling. Consequently, they were almost always removed from further analyses (see Chapter 6).

The second step consisted in removing hair beneath each optode to avoid light obstruction. A stylus with a LED light was used to spread the hair in each optode hole. More precisely, the hair was pushed back and wedged under the edge of the optode hole by means of a gentle pressing. This operation was repeated several times until the participant's scalp was clearly visible. Furthermore, a system calibration was performed through an automatic adjustment using LabNIRS (Shimadzu, Kyoto, Japan) to ensure that sufficient amount of light could be detected by detector optodes (i.e., absence of light obstruction). If necessary, the hair was pushed back once again beneath each identified optode until the automatic adjustment was satisfactory.

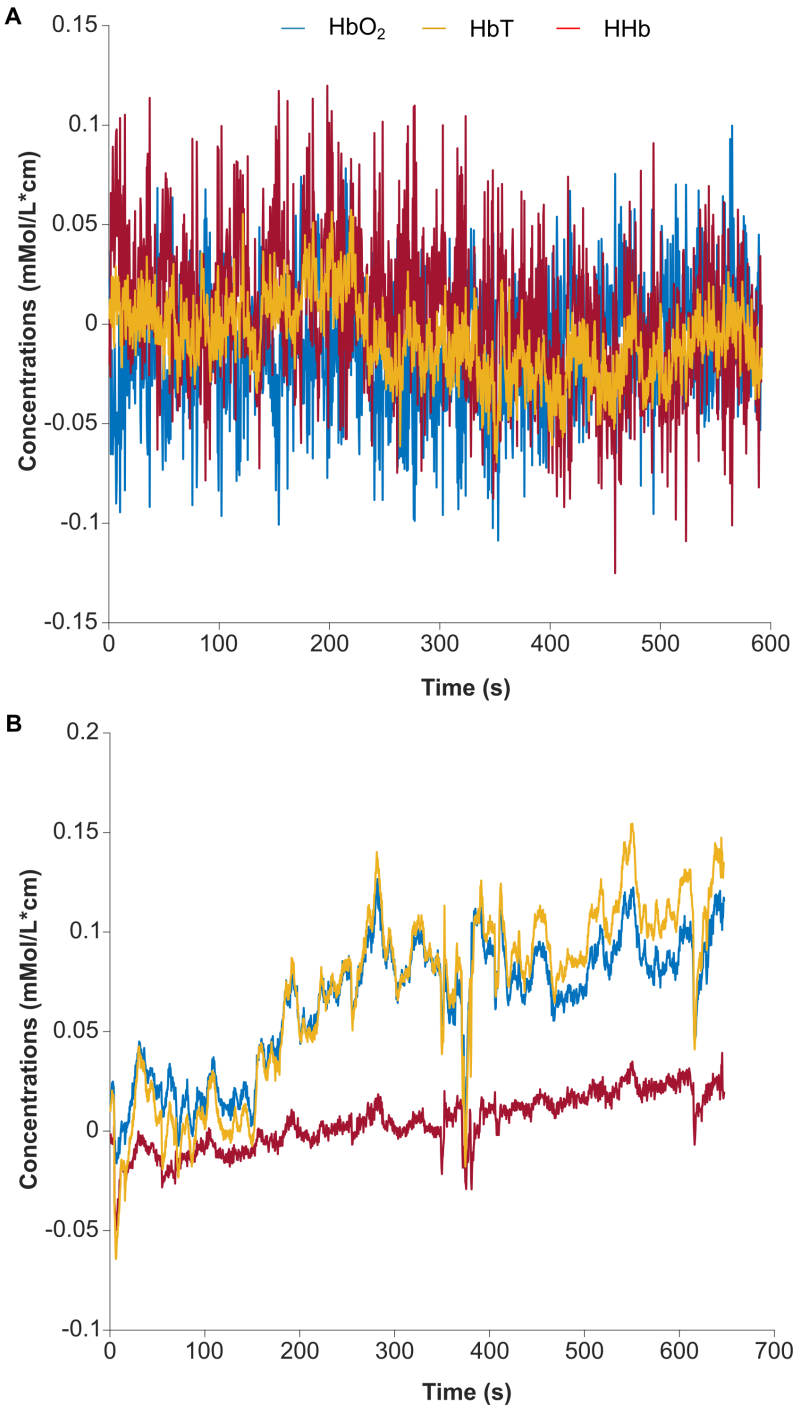
The implementation of this two-step procedure facilitated the acquisition of high-quality *f*NIRS data using participants that had hair. We were ultimately able to acquire *f*NIRS data of the same quality than those obtained using participants with shaven heads (see Chapters 6 and 7).

2.3.2 *Detection of Headset Shifts*

In neuroimaging studies, careful attention is given to the location of recording sensors over the cerebral region of interest. In the studies of the present programme of work, the International 10–20 system guidelines (Jasper, 1958) was adopted in terms of placement of the *f*NIRS headset (Okamoto et al., 2004). The nasion–inion

Figure 3

Raw fNIRS Data from a Participant With Hair vs. a Participant Without Hair



Note. Raw data for HbO_2, HHb and HbT. Panel A: A typical participant with hair. Panel B: A typical participant without hair. HbO_2 = oxygenated haemoglobin; HHb = deoxygenated haemoglobin; HbT = total haemoglobin.

(from nasal bridge to occipital protuberance) and bilateral pre-auricular (from left pre-auricular to right pre-auricular) distances were measured for each participant. The reference optode was located at the midway point between the two distances.

The general aim of my thesis was to examine the brain mechanisms germane to time production; accordingly, the experimental tasks used in each study entailed some form of movement. A serious complication is that performing a motor task (e.g., walking or cycling) can easily result in a shift in the *f*NIRS headset. If a headset shift occurs during an experimental session, the exact source of recorded haemodynamic signals is rather difficult to determine.

An important methodological precaution of my *f*NIRS studies was to use a motion capture technique (Qualisys MoCap, Götebord, Sweden) to detect shifts in the *f*NIRS headset. To this end, two retro-reflective markers were taped to the headset and one to the participant's right temple. The basic principle being that the area connecting the three markers (referred to as the *mesh area*) should remain consistent. A fluctuation of the mesh area is indeed indicated of a shift of the headset markers in relation to the temple marker.

A motion capture recording provides Cartesian coordinates (i.e., x, y, and z) for each marker. The mesh area between the three markers M_i, with $i \in \{0; 1; 2\}$, at a given moment in time $t \in [1; d]$, with d defined as the acquisition duration, was computed using a scalar product (Equation 1), equal to twice the mesh area (S):

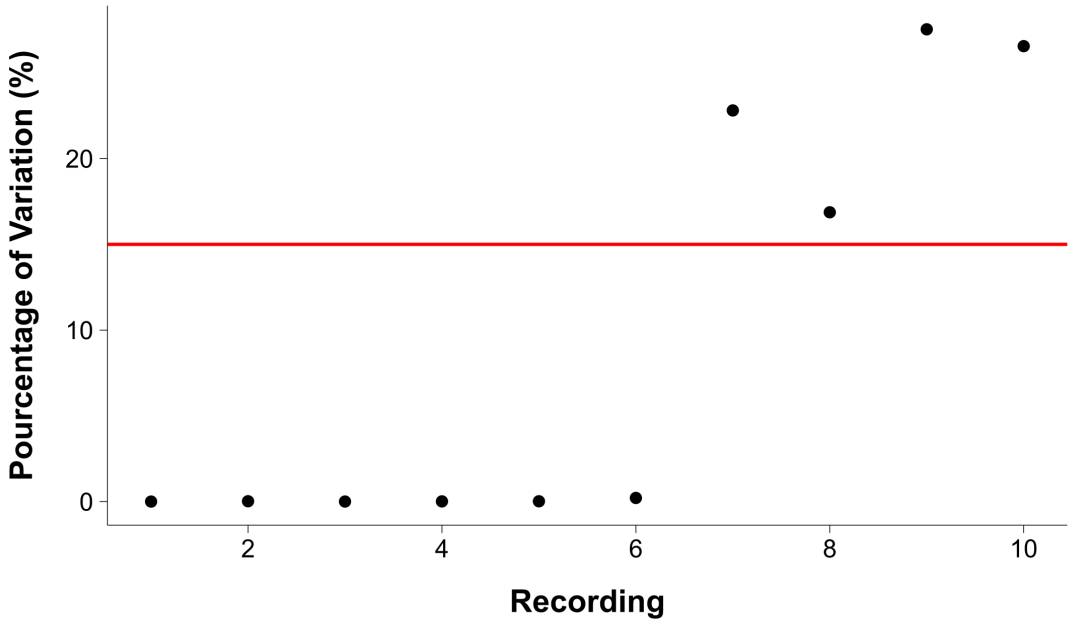
$$2S = \overrightarrow{M_0M_1}(t) \cdot \overrightarrow{M_0M_2}(t) = \begin{pmatrix} x_1(t) - x_0(t) \\ y_1(t) - y_0(t) \\ z_1(t) - z_0(t) \end{pmatrix} \cdot \begin{pmatrix} x_2(t) - x_0(t) \\ y_2(t) - y_0(t) \\ z_2(t) - z_0(t) \end{pmatrix} \tag{1}$$

If $\overrightarrow{M_0M_1} \cdot \overrightarrow{M_0M_2}$ remained constant over time with an acceptable error threshold, an absence of deformation of the mesh was considered and indicative of an absence of headset shift. The error threshold ϵ was set to 10 mm, which corresponds to the degree of spatial resolution of the *f*NIRS technique (Quaresima & Ferrari, 2016). The variation Δ_{mesh} of the $\overrightarrow{M_0M_1} \cdot \overrightarrow{M_0M_2}$ value between two moments in time was then computed. An *f*NIRS headset shift occurred if this value exceeded 15%, which corresponds with ϵ.

A pilot test was undertaken to verify the suitability of motion capture to detect small variations in the mesh area. The *f*NIRS headset and the three markers were installed on a polystyrene head to ensure complete stability. The polystyrene head was placed on a steady stool, and five recordings of 60 s were performed. Between each recording, a new calibration of the motion capture system was performed. Δ_{mesh} was then computed for each recording to obtain the reference value of the motion capture system. The average variation was 0.013% (min = 0.003%; max = 0.022%).

Five 60-s recordings were also performed using a participant. During the first recording, the participant was required to stand still. The computed Δ_{mesh} was 0.214%, which is close of the mean value found using the polystyrene head. During the last four recordings, an *f*NIRS headset shift was provoked (i.e., forward shift, backward shift, left-lateral shift, and right-lateral shift) at ~15 s. For each type of shift, Δ_{mesh} was > 15% (backward shift = 27.540%; forward shift = 22.810%; left-lateral shift = 26.558%; right-lateral shift = 16.870%; see Figure 4).

Figure 4
fNIRS Headset Shift Tests



Note. The red line indicates the *f*NIRS headset shift threshold.

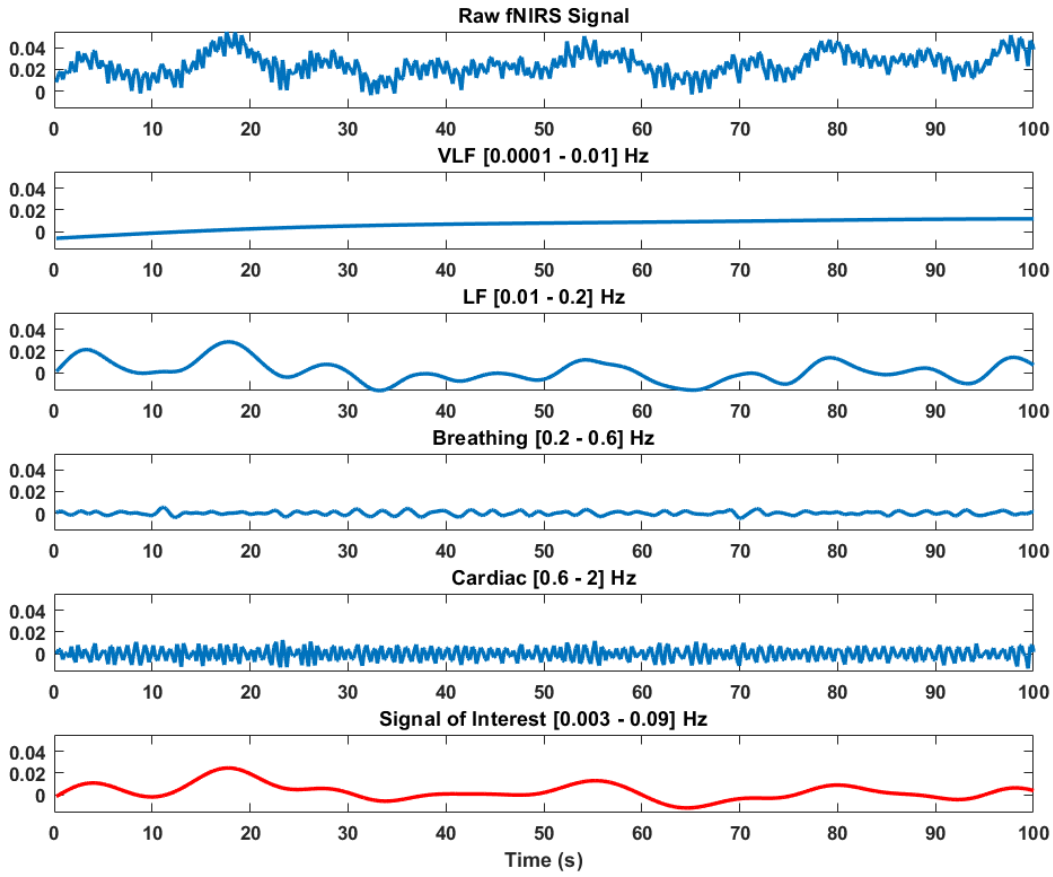
The computation of Δ_{mesh} enables the researcher to detect the occurrence of a significant *f*NIRS headset shift throughout an experimental session. Moreover, this approach allows to know precisely *when* the headset shift occurred. In my studies, if an *f*NIRS headset shift was detected, the data from the corresponding participant were removed prior to further analyses (see Chapter 6).

2.3.3 *Channel Selection*

The *f*NIRS system used in the present programme of research is a multi-channel device, with 16 sources (multicomponent glass bundle fibers) and 16 detectors (multialkali photomultipliers detectors). An *f*NIRS channel is composed of a source–detector pair; a maximum of 47 measurement channels can be assembled for a whole-head coverage. Nonetheless, some channels suffer from a low signal-to-noise ratio (e.g., due to poor optical coupling), resulting in noisy *f*NIRS signals. Thus, checking the quality of the raw *f*NIRS signal for each channel is a crucial preprocessing step. A complication is that there is currently no consensus regarding an automated preprocessing routine among *f*NIRS neuroscientists (see Dans et al., 2021; Hocke et al., 2018; Pfeifer et al., 2018). I chose to rely on the presence of physiological noise to check the quality of *f*NIRS signals, as recommended by Pinti et al. (2019).

The *f*NIRS technique measures cerebral oximetry, which is strongly associated with respiratory and cardiac functioning. If the recorded *f*NIRS signal is legitimate, it should contain physiological components (e.g., heart and respiratory rates; see Figure 5) – otherwise the recording might be noise emanating from instrument or

Figure 5
Decomposition of fNIRS Signal Components



Note. VLF = very low frequency; LF = low frequency.

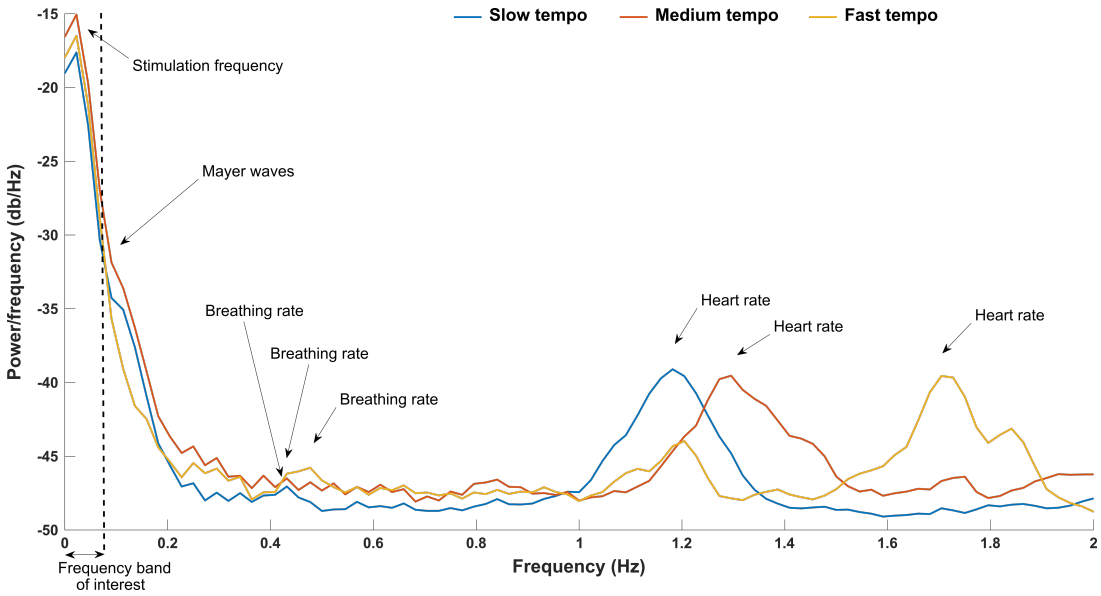
environment. Spectral analysis was undertaken to detect heart and respiratory rates in the *f*NIRS signal. More specifically, Welch's estimation method was used to compute the power-spectrum density (PSD) for each channel. The signal was considered of sufficient quality if the heart rate was clearly visible (see Figure 6). Channels with a poor-quality signal were removed prior to further analyses. In my *f*NIRS studies, the number of channels eliminated was reported in a systematic manner in the interest of research transparency.

Several peaks can occasionally be present in the power spectral density. For example, two possible heart rate peaks were found at 1.2 and 1.7 Hz in Figure 6 for the fast-tempo condition (in yellow). To ensure that the detected peak corresponded to the participant's heart or respiratory rate, cardiac and respiratory activities were recorded by means of the Biopac equipment (Biopac Systems, Goleta, CA). Indeed, the combination of *f*NIRS measurement with physiological recordings has been advocated in recent years and referred to as systemic-physiology-augmented *f*NIRS (SPA-*f*NIRS; Scholkmann et al., 2017).

Heart and respiratory rates were computed, and compared to the peaks detected in the power spectrum density of the *f*NIRS signal. It is worth mentioning that the

Figure 6

Power-Spectral Density Computed on Raw fNIRS Signals



Note. Raw oxygenated haemoglobin data for the three experimental conditions. These data were obtained from a pre-test during which a participant had to performed a cycling task at fast, medium, and slow paces.

physiological components were ultimately filtered to isolate the brain's haemodynamic response. Nonetheless, ensuring the presence of physiological components is an important step in *f*NIRS data analysis.

2.3.4 *Defining Valid Trials*

Brain imaging provides insight into the cerebral processes underlying the execution of a given behaviour. The task eliciting the studied behaviour must be performed properly, otherwise the recorded brain activity will not be informative to the researcher. Monitoring the participant's conduct is thus as important as monitoring their brain responses.

In the present programme of research, participants were required to perform motor tasks at different paces. The accuracy of the sensorimotor synchronisation (i.e., asynchrony and/or IRI_{error}) was computed in each experimental study. An arbitrary threshold of 70% level was adopted. If the behavioural accuracy was lower than the threshold (i.e., invalid trial), the *f*NIRS data pertaining to the associated trials were removed from further analyses. The number of eliminated trials were systematically reported for each study.

It should be emphasised that the non-elimination of invalid trials can modify the outcome of a study. In Chapter 4, the significant difference in motor activation found between the slow and fast experimental conditions was absent when behavioural checking was not performed. More specifically, the absence of difference did not

arise from an absence of motor speed effect over the motor areas – this effect is well reported in the scientific literature (see Kuboyama et al., 2004; Kuboyama et al., 2005). Rather, the absence of effect was due to the average of brain responses that were different because they did not underlie the same performance levels. Precisely, data from correct movement (i.e., in conformity task instructions) were averaged with data from too slow/fast movements (i.e., not in conformity with task instructions). Such unconsidered averaging led to an increase in haemodynamic-response variability. Ultimately, the difference in motor activation between fast and slow movements was obliterated.

The methodological guidelines presented in this Chapter were followed for the studies presented in my thesis. I hope that they will be valuable resources for future young scientists, especially those engaging in the use of *f*NIRS brain measurements during whole-body movements.

Part III

EXPERIMENTAL AND THEORETICAL CONTRIBUTIONS

3

COGNITIVE CONTROL ENGAGEMENT WHEN MOVING FAST AND MOVING SLOW

Published as Guérin, S. M. R., Boitout, J., & Delevoye-Turrell, Y. N. (2021a). Attention guides the motor-timing strategies in finger-tapping tasks when moving fast and slow. *Frontiers in Psychology*, *11*, Article 574396. https://doi.org/10.3389/fpsyg.2020.574396.

3.1 INTRODUCTION

A captivating aspect of human behaviour is that most of our everyday life actions share a similar temporality. In the past 50 years, psychological sciences have confirmed the existence of a preferred tempo, referred to as the spontaneous motor tempo (SMT), which is the most natural and easiest pace at which to move (Fraisse, 1974; Fraisse et al., 1954; Moelants, 2002). The SMT is found to average ~2 Hz in adult populations (McAuley et al., 2006; Moelants, 2002). This particular motor signature is slightly faster in children and slower in elderly individuals, but remains strikingly close to two movements per second, even across tasks of different levels of complexity (e.g., finger tapping, foot stomping, hand clapping; Baudouin et al., 2004; Provasi & Bobin-Bègue, 2003; Rose et al., 2020).

Delevoye-Turrell et al. (2014) found that repetitive cyclic movements (e.g., finger-tapping and cycling tasks) were accomplished with greater accuracy and better stability when performed at the SMT when compared to execution at faster or slower tempi. Interestingly, studies on locomotion (e.g., walking or running) indicated that the SMT is also associated with a more efficient metabolic energy consumption (Holt et al., 1995; Sparrow & Newell, 1994). Movements that were faster or slower than the SMT were associated with greater energy expenditure. This phenomenon may be due to fact that the ability to modulate the pace of spontaneous motor behaviours requires control.

Experimental evidence shows that humans beings have a clear ability to synchronise the pacing of their actions with external events (Bryant & Barrett, 2007; Kirschner & Tomasello, 2009). With experience, children learn to adapt their SMT to match the pace of surrounding entities, such as their parents' behaviours (Brazelton et al., 1975). Accordingly, this is not an innate ability. Bobin-Bègue and Provasi (2008) reported that very young children (i.e., 1½- and 2½-year-olds) were capable neither to accelerate nor to decelerate the pace of their action. These findings indicated that adjustments in motor timing required some sort of cognitive control that was not yet available to very young children. Interestingly, 3½-year-olds were able to accelerate but not slow down the pacing of their movements – they were able to tap in rhythm with fast-paced auditory metronomes but not with slow ones.

The pattern of results obtained by Bobin-Bègue and Provasi (2008) indicated that the capacity to slow down the tempo of voluntary movements appears later

in life than the capacity to accelerate. This developmental asymmetry described in children may be due to the later maturation of frontal executive functions, which would be needed to decelerate self-initiated actions according to externally-imposed metronomes (Provasi & Bobin-Bègue, 2003). More specifically, inhibitory capacities might be involved to stop the urge to move as fast as the SMT. As an example, this is what happens during downhill walking, for which the pace of walking tends to increase through the simple dynamic shift of body weight. In such circumstances, motor inhibition is required if one wants to maintain a slower pace.

In the field of cognitive psychology, early studies claimed that the pacing of motor behaviours was underpinned by a central temporal mechanism, seen as a general skill (Franz et al., 1992; Keele et al., 1985). With a resonance of such thinking, the internal clock model conceptualised the processing of time using cognitive entities: a pacemaker, counter, store, and comparator (Treisman, 1963). This pacemaker-accumulator model is composed of three distinct stages in which temporal information are extracted, encoded, and processed. In addition, this model includes a motor component to account for peripheral variance (Wing & Kristofferson, 1973b). Accordingly, time production can be modelled following Equation 2:

$$I_i = C_i + M_i - M_{i-1} \tag{2}$$

where i is a time interval, I is the series of time intervals, C is a central source of variance related to the generation of time intervals by the internal clock, and M is a peripheral source of variance that reflects motor delay.

Motor timing seems to depend on four cognitive components that serves to adjust the production of voluntary motor actions using an explicit representation of time interval. Given that this representation is cognitive in nature, it requires attentional resources. However, the results reported by Provasi and Bobin-Bègue (2003) suggest an asymmetry in the development of temporal control processes, with an earlier maturation of functions for motor acceleration than for motor deceleration. This asymmetry in timing abilities for slow and fast actions in children could be due to the involvement of two separate timing strategies.

Over the past two decades, researchers have advocated the existence of two temporal control processes (Robertson et al., 1999; Zelaznik et al., 2000). Zelaznik et al. (2002) distinguished explicit from implicit strategies, later renamed *predictive* and *emergent* timing, respectively (Ivry et al., 2002; Spencer & Ivry, 2005). While predictive timing would rely on the internal clock model (Treisman, 1963), emergent timing would depend on the implicit emergence of temporal regularities, from the kinetic parameters that are inherent to body dynamics (e.g., mass, length, velocity; Zelaznik et al., 2002).

Within the dynamical systems framework, emergent timing is the result of the interaction between the individual, their environment, and the physical constraints of the behavioural task. Emergent timing was modelled by Delignières et al. (2004) following Equation 3:

$$I_i = D_i + \xi_i \tag{3}$$

where i is a time interval, I is the series of time intervals, D is the self-sustained oscillatory frequency, and ξ is a Gaussian white noise accounting for the variability inherent to biological systems.

A striking difference between the two timing strategies is their capacity to correct timing errors. Cognitive control is required for the detection and implementation of error corrections. Hence, only the predictive timing mode should be in the capacity to correct timing errors during ongoing motor activities. The autocorrelation (AC) analyses have been used by researchers to examine error corrections in interval timing production. Oscillatory movements (e.g., circle drawing) are predominantly performed using emergent timing (Vorberg & Wing, 1996; Wing & Kristofferson, 1973a). As emergent timing does not support a correction process, the series of time intervals (i.e., inter-response interval, IRI) were characterised by positive or close-to-zero ACs (Robertson et al., 1999; Studenka & Zelaznik, 2008). Thus, an n interval that is too short can be followed by a even shorter $n+1$ interval.

On the other hand, tasks affording predictive timing (e.g., tapping tasks) were characterised by the presence of error-correction mechanisms: An n interval that was too short was followed by a longer $n+1$ interval, and vice versa (Robertson et al., 1999; Studenka & Zelaznik, 2008). The IRI series were in this case characterised by negative ACs. Therefore, temporal strategies can be distinguished at a behavioural level according to the shape of their error distributions.

Emergent and predictive timing are generally described as mutually exclusive strategies, depending on the features of the performed movements (Robertson et al., 1999): Predictive timing is peculiar to discrete movements (i.e., with no clearly distinguishable beginning and end), and emergent timing to continuous movements (i.e., with no recognisable beginning and end; Schmidt et al., 1988). Yet, it has been suggested that the task is not a key point in the distinction between the two timing strategies. Some behavioural tasks were indeed found to involved both timing modes (Huys et al., 2008; Madison & Delignieres, 2009).

An example entails the air-tapping task, which involves voluntary tapping movements that do no entail surface contact. When participants were required to perform this task at their SMT, Delignieres and Torre (2011) reported that the temporal control mode was emergent (i.e., positive ACs), predictive (i.e., negative ACs), or hybrid (i.e., close-to-zero ACs) according to the timing strategy adopted by each individual. Accordingly, the use of one or other of the timing strategies is dependent not on the *nature* of the task, but on the *way* participants perform the task (i.e., whether or not they use an explicit representation of the temporal intervals).

The time pressure set upon the execution of a voluntary movement may be a factor that orients the timing strategy that is employed. During an air-tapping task in synchronisation with a metronome, Huys et al. (2008) reported that movements were less discrete when an external metronome constrained participants to increase motor tempo. Similar results were found using a spatial finger-tapping task, which is a hybrid task that combines the requirements of the finger-tapping and circle-drawing tasks (Dione & Delevoye-Turrell, 2015). When required to tap successively on six targets arranged in a circle following the pace given by a metronome, participants were found to use emergent timing for fast tempi (i.e., faster than the SMT), and predictive timing for slow tempi (i.e., slower than the SMT).

Findings from Dione and Delevoye-Turrell (2015) suggest that the alternation of the two timing modes depends on the temporal constraints inherent to the task. Nonetheless, ACs were computed over the entire trial, which is more prone to bias

than moving-average time series analysis (Delignieres & Torre, 2011). In addition, ACs analysis alone is not sufficient to disentangle the involvement of cognitive control for time production.

The general aim of this chapter was to examine the role of the cognitive control in emergent and predictive timing using (a) time series analysis and (b) a dual-task paradigm. The classic finger-tapping task (simple one-target pattern) and the spatial finger-tapping task (complex six-target pattern) were used to assess the effects of both time constraints and motor complexity on the alternating use of predictive and emergent timing strategies. The two finger-tapping tasks were administered via a computer touchscreen according to externally-paced tempi ranging from 300 to 1100 ms.

In Study 1, detrend windowed autocorrelations (DWA; Lemoine & Delignières, 2009) was used to confirm the alternating involvement of predictive and emergent timing as a function of motor tempo. I hypothesised that slow tempi would solicit predictive timing (i.e., negative lag-1 ACs), whereas fast tempi would solicit emergent timing (i.e., positive or close-to-zero lag-1 ACs; $H1$). The complexity of the motor task being undertaken would not significantly impact the use of one or other of the timing strategies ($H2$).

In Study 2, a dual-task paradigm was designed to examine the attentional resources needed to perform the finger-tapping task under contrasting time and task complexity constraints. I hypothesised that action production at slower tempi would lead to longer reaction times when compared to task execution at faster tempi ($H3$). Furthermore, finger tapping would be associated with shorter reaction times when pointing to the one-target than the six-target visual pattern, as the latter requires the control of hand movements through space and time ($H4$).

3.2 STUDY 1

Autocorrelation (AC), sometimes known as serial correlation, is the correlation of a time series with a delayed copy of itself. That is, ACs measure the similarity between observations as a function of the time lag between them. The AC function can be used to detect non-randomness in the data and thus identify any cyclic patterns. In the present case, the aim was to reveal cyclic patterns of time intervals produced in synchronisation with an external pacing metronome.

An AC is very similar to a Pearson product-moment correlation coefficient. However, instead of being computed between two different variables, the coefficient is calculated between two values of the same variable at two moments in time, X_t and X_{t+k}. The resulting values are usually plotted for different lags k in a so-called correlogram.

The use of AC analysis in timing research was originally proposed by Wing and Kristofferson (1973a) to measure the variance of predictive model components. Thereafter, Lemoine and Delignières (2009) adjusted the mathematical approach to develop the DWA method. This approach provides the means to reveal the use of emergent and predictive timing in short time series (i.e., 128 data points), with less bias and variability than other similar techniques (e.g., spectral analysis; Delignieres et al., 2006). Using the DWA method, Delignieres and Torre (2011) were able to highlight

positive windowed lag-1 ACs in continuous movements, and negative windowed lag-1 ACs in discrete movements.

In the present study, the DWA method was used to confirm that two different timing strategies were implemented as a function of the constrained speed of motor execution. If two different motor timing strategies are used to produce pointing actions at fast and slow pace, the modelling of the redundant cyclic patterns through DWA should provide distinct patterns of time series.

3.2.1 *Material and Methods*

3.2.1.1 *Participants*

The sample size required for the present study was calculated using G*Power (3.1.9.2). The theoretical sample size was computed for a repeated-measures analysis of variance (RM ANOVA), with the lag-1 ACs results of Dione and Delevoye-Turrell (2015) as group parameters. The power analysis indicated that a minimum of 20 participants would be required (f = .56; α = .05; 1-β = .80). An additional five participants were recruited in case of deletions due to outliers.

Twenty-five right-handed participants between 18 and 35 years (M_{age} = 21.6, SD = 1.4) participated voluntarily in the study. Each of them received an information sheet, and completed a written informed consent. Participants reported having normal or corrected-to-normal vision and no deficiencies in terms of motor control.

The small telescopes approach was used to determine the SESOI (i.e., the difference that is considered too small to be meaningful; Simonsohn, 2015). Accordingly, the SESOI was set to the effect size that an earlier study would have had 33% power to detect (Lakens et al., 2018). As previously, the lag-1 AC results of Dione and Delevoye-Turrell (2015) were used as group parameters. The sensitivity analysis indicated that an effect size of at least f = .09 (i.e., η_p^2 = .01) was required yield meaningful results.

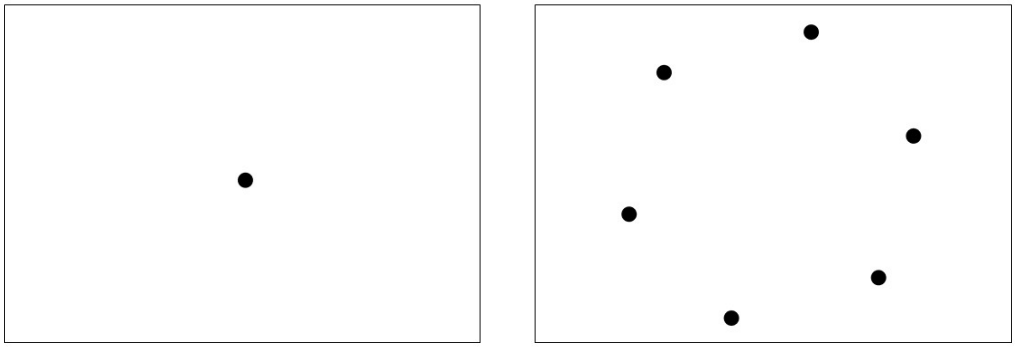
3.2.1.2 *Tasks Description and Materials*

Participants were administered two finger-tapping tasks on a touchscreen using the right index finger, with a closed fist. The touchscreen (1915L Elo Touch 19"; Elo Touch Solutions Inc.; Milpitas, California, CA) was placed on a table in front of the participant, with the screen oriented at 45°. The participant was seated on a stool, which was suitably adjusted to their height to minimise muscular fatigue and optimise comfort.

In the one-target condition, the participant was required to tap on a single target (10-mm-diameter black dot) displayed in the centre of the screen (Figure 7, left panel). In the six-target condition, six targets (10-mm-diameter black dot) arranged in a circle pattern (100-mm radius) were displayed on the screen (Figure 7, right panel). The participant was instructed to tap each target one after the other starting from the top-right target, and moving counterclockwise.

In both tasks, the participant was asked to synchronise their finger taps with the auditory cues given by a metronome. The beeps of the metronome (duration = 80 ms; sound frequency = 294 Hz) were played through Creative SBS 250 desk

Figure 7
Experimental Materials



Note. Illustrations of the visual stimuli for the one-target (left), and the six-target conditions (right).

speakers that were placed on both sides of the screen. The beeps indicated inter-stimuli intervals (ISIs) of either 300, 450, 600, 800, or 1000 ms. These fast and slow metronome paces enabled the participant to depart from their SMT, but to remain within the possible sensorimotor synchronisation (SMS) zone (between 180 and 1800 ms; Keele et al., 1985). The auditory stimuli were generated using MATLAB 7.11.0 R2010 software (Mathworks Inc.; Natick, Massachusetts, MA).

3.2.1.3 *Procedure*

A within-subjects design was applied wherein each finger-tapping task was performed in a fully counterbalanced order. For each of the two tasks, ISIs were presented with increasing time intervals on each task for half of the participants (i.e., from 300 to 1000 ms), and with decreasing time intervals for the other half (i.e., from 1000 to 300 ms). A trial consisted in 180 beeps. Overall, participants performed a total of 10 trials. The total duration of the experimental test period was ~45 min. Participants were systematically debriefed at the end of the session.

3.2.1.4 *Data Acquisition and Processing*

INTER-RESPONSE INTERVALS. IRIs were measured as the time interval between the onset of successive taps. Before calculating accuracy indicators and windowed lag-1 ACs, the series of taps were checked to detect and remove the IRIs greater than twice the ISIs of a given trial. Overall, 0.16% of the data were removed from the analysis. These trials were referred to as temporal omissions and not included in further analyses.

ACCURACY INDICATORS. In order to confirm that participants performed the finger-tapping tasks accurately, timing and spatial errors were computed. Relative asynchrony (ms) was calculated as the absolute time difference between the tap and the beep, divided by the ISI. Thus, the relative absolute asynchrony within a trial was used as an indicator of synchronisation accuracy that takes into account the scalar

property of timing (i.e., larger time intervals generate more errors; see Rakitin et al., 1998).

Spatial error (pixels) was computed as the difference between the centre of the visual target and the location of the participant's fingertip. The mean pointing error within a trial was used as an indicator of spatial accuracy.

DETREND WINDOWED AUTOCORRELATIONS. The DWA procedure was used to reveal the evolution of lag-1 ACs within a trial (Lemoine & Delignières, 2009). This procedure provided the means by which to reduce the frequent bias and high variability observed within lag-1 ACs (Delignieres et al., 2006). Windowed lag-1 ACs were computed for each trial as follows: A window corresponding to the first 30 IRIs of a trial was selected and the linear trend of this window removed. Then, the lag-1 AC was calculated. This procedure was repeated after shifting the window by one IRI event. This method was applied until the moving window had scanned the entire time series. A total of 150 windowed lag-1 ACs were computed per trial. Finally, the mean windowed lag-1 AC was computed, and used as an indicator of the dominant timing mode used for a given trial.

3.2.1.5 *Statistical Analysis*

To monitor motor performance in the two visuomotor tasks, absolute asynchronies and spatial errors were submitted to a twoway RM ANOVA (Task [one target, six targets] × ISI [300, 450, 600, 800, 1000]). To examine H_1 and H_2, the mean windowed lag-1 ACs were also submitted to a two-way RM ANOVA. Normality was checked using the Shapiro–Wilk test. Where Mauchly's tests indicated violations of the sphericity assumption, Greenhouse–Geisser adjustments were applied. Tukey post hoc tests were used as necessary. Statistica (v.13.1) was used for the statistical analyses, with alpha set at $p < .05$.

3.2.2 *Results*

3.2.2.1 *Descriptive Results*

Mean absolute asynchronies and spatial errors are presented in Table 1. Overall, participants were able to perform the two visuomotor tasks accurately following both time and space constraints.

SYNCHRONISATION ACCURACY. The main effect of task was significant, $F(1, 24) = 11.10$, $p = .003$, $\eta_p^2 = .32$, with a smaller relative asynchrony in the one-target ($M = 110$, $SD = 65$) than in the six-target condition ($M = 142$, $SD = 83$). Neither the main effect of ISI nor the ISI × Task interaction were significant. Overall, these results indicated that the participants made more timing errors when the motor task was complex.

SPATIAL ACCURACY. The RM ANOVA indicated a significant main effect of ISI, $F(4, 96) = 55.26$, $p < .001$, $\eta_p^2 = .70$, with smaller spatial errors in the 600, 800, and 1000 ms ISI conditions ($M = 8.4$, $SD = 2.6$) than in the 450 ms ($M = 9.1$, $SD = 2.1$) and

Table 1
Synchronisation and Spatial Indicators for Study 1

Indicator	One-target pattern					Six-target pattern				
	300 ms	450 ms	600 ms	800 ms	1000 ms	300 ms	450 ms	600 ms	800 ms	1000 ms
Relative asynchrony	110	113	115	116	95	149	133	157	153	120
Spatial error	7.8	7.7	8.4	8.4	8.8	16.3	10.5	9.1	7.8	7.8

Note. Relative asynchrony (ms) and spatial error (pixel) for each inter-stimuli interval and each task.

in the 300 ms ISI conditions (M = 12.0, SD = 2.9). The main effect of task was also significant, $F(1, 24) = 32.58$, $p < .001$, $\eta_p^2 = .58$, with smaller spatial errors in the one-target (M = 8.2, SD = 3.0) than in the six-target condition (M = 10.3, SD = 2.1). The ISI $\times$ Task interaction was significant, $F(4, 96) = 72.39$, $p < .001$, $\eta_p^2 = .75$. This interaction indicated that spatial errors were smaller in the one-target vs. the six-target condition, but only in the 450 ms ($p < .001$) and 300 ms ISI conditions ($p < .001$). Nonetheless, pointing errors were greater in the one-target vs. the six-target condition in the 1000 ms ISI ($p = .030$). Overall, these results indicated that participants made more spatial errors when the motor task was complex, and particularly so under high speed of execution.

3.2.2.2 *Mean Windowed Lag-1 ACs*

The RM ANOVA revealed only a significant main effect of ISI, $F(4, 96) = 5.08$, $p < .001$, $\eta_p^2 = .17$, with more negative mean windowed lag-1 ACs in the 1000 ms ISI (M = -0.23, SD = 0.12) vs. 300, 450, 600, and 800 ms ISI (M = -0.15, SD = 0.13). Neither the main effect of task nor the ISI $\times$ Task interaction were significant. Note that the effect size of the ISI main effect was greater than the required SESOI, which indicated that the effect was large enough to be considered as meaningful. Thus, the slower tempo induced more negative mean windowed lag-1 ACs (Figure 8) and this effect was similar across both tasks.

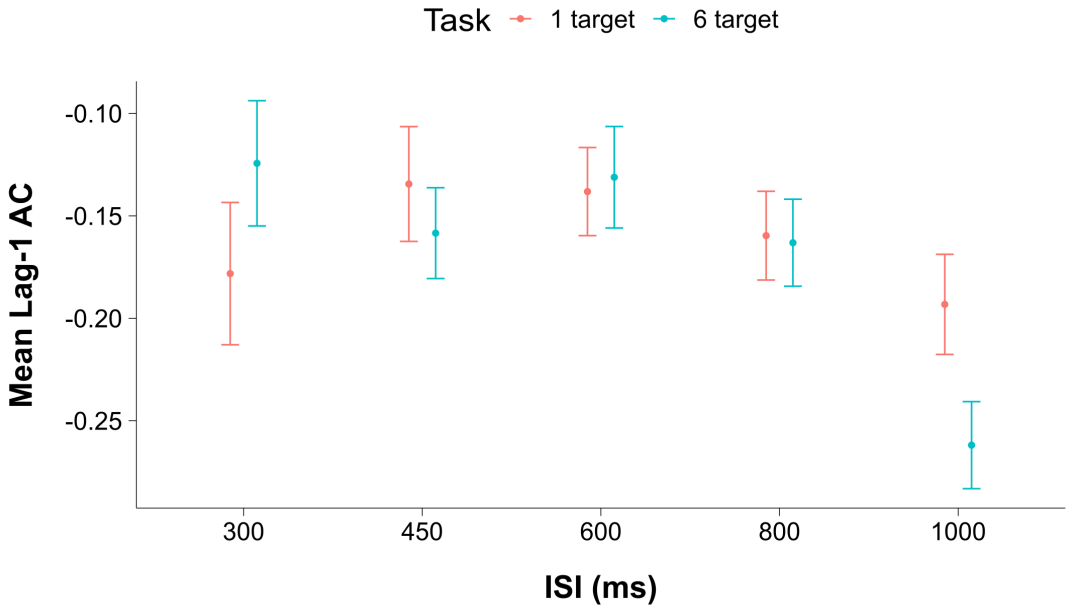
3.2.3 *Discussion*

The purpose of Study 1 was to examine the timing strategies used under different time and space constraints through the use of time series. The reported data showed that slow tempo favoured negative ACs (i.e., predictive timing), regardless of the movement complexity. Notwithstanding this finding, compared when participant where cued to move slowly, ACs were less negative when participants were instructed to move at fast or close-to-SMT paces. This pattern of results was consistent with an emergent timing strategy that is characterised by an absence of corrective processes (Studenka & Zelaznik, 2008).

There was a general tendency towards negative ACs in the present study. This observation was in line with previous studies using finger-tapping tasks (Pollok et al., 2005; Repp, 2005). The negative ACs confirmed the general need of cognitive processes for motor control, even in the simplest movements (Delevoye-Turrell et al.,

Figure 8

Autocorrelations Results for Each Experimental Condition



Note. Mean lag-1 ACs for each inter-stimuli interval. Errors bars represent 95% confidence intervals. AC = autocorrelation; ISI = inter-stimuli interval.

2006). This phenomenon was probably due to the very nature of the tapping tasks, which requires the production of a series of discrete actions. Each finger movement had a distinct start and end, corresponding to the finger-screen contact duration. Hence, tapping can be considered a cognitive task that required the continuous updating of motor commands by feedback loops (Desmurget & Grafton, 2000; Guigon et al., 2008). However, these implementations took time; the findings that ACs were more negative at slow tempo suggest that in the absence of time constraints, predictive timing strategies can be implemented efficiently to further decrease both timing and spatial errors.

Overall, the results of Study 1 confirm that windowed lag-1 AC analysis is a mathematical approach that is powerful enough to reveal changes in the cognitive strategies for motor timing. The DWA may be a proper tool to investigate the conditions triggering the alternation between emergent and predictive timing for adapted motor behaviour. A key benefit of this method is that it takes into consideration the evolution of motor timing strategies (Delignieres & Torre, 2011), giving access to a sensitive analysis that avoids blurring of the data due to a single-averaging approach performed across an entire series. The data of Study 1 supported the hypothesis that different timing strategies are implemented depending on the speed constraints of the performed movements. However, they do not elucidate the cognitive nature of the timing process involved.

Past developmental research has suggested that executive functions are influential to modulate the speed of motor execution and, in particular, slow down the spontaneous pace of voluntary motor actions (Provasi & Bobin-Bègue, 2003). A possible

explanation is that the execution of slow movements requires further attentional resources to have an explicit representation of and to memorise the time intervals to be produced. Thus, predictive timing would involve working memory to compare the reference interval and the interval that is to be produced, at each step of the timing sequence (Treisman, 1963). In Study 2, the aim was to examine the attentional cost associated with predictive motor timing. My primary hypothesis was that moving slower than the SMT should require more cognitive resources than moving faster or close to the SMT.

3.3 STUDY 2

Compared to other areas within cognitive neurosciences, it might appear that the mechanisms controlling our actions should be readily understood. The motor action outcome communicates the goal of the action and gives access to its biological significance. However, adaptive movement involves much more than the contraction of a pre-defined sequence of muscles. Well-adjusted motor actions must be informed, not only by the constraints of the environment in which the movement is performed, but also knowledge of the biological system limits. This implementation is cognitively demanding, even for simple actions performed a thousand times a day. The aim of Study 2 was to examine the attentional demands of moving at various paces by means of a dual-task paradigm.

One of the most used experimental paradigms in psychology to reveal the attentional demand of an activity is the dual-task paradigm, which consists in performing a task of interest concurrently with a secondary task. Because attentional resources are finite, the more expensive the primary task is in attentional terms, the more the behavioural performance of the secondary task is impaired (Kahneman, 1973). The dual-task paradigm illustrates that attention is allocated on a moment-by-moment basis depending on task requirements. Through the years, experimental studies have demonstrated that the dual task paradigm is a valuable tool in addressing the dynamic nature of attention, managed by top-down control processes (Delevoye-Turrell et al., 2006; Karatekin et al., 2004).

In Study 2, participants performed the same finger-tapping tasks as in Study 1 (i.e., primary task). The visuomotor sequences were to be performed in synchrony with tempi ranging from 300 to 1100 ms. In addition, a simple reaction-time task was included (i.e., secondary task). Finger pressure was also recorded to monitor levels of motor contraction, which reflected the degrees-of-freedom and thus the control strategy applied to limb movements.

3.3.1 *Material and Methods*

3.3.1.1 *Participants*

The sample size required for the present study was calculated using G*Power (3.1.9.2; Faul et al., 2007). The theoretical sample size was computed for a RM ANOVA. In the estimation of effect size, the dual task results of Brünken et al. (2004) were used as group parameters. The power analysis indicated that a minimum of 23 participants

would be required (f = .51; α = .05; 1-β = .80). An additional two participants were recruited in case of deletions due to outliers.

Twenty five right-handed participants in the age range 18–35 years (M_{age} = 23.3, SD = 3.2) participated voluntarily in the study. Each received a participant information sheet and completed a written informed consent. Participants reported having normal or corrected-to-normal vision and no deficiencies in terms of motor control.

As in Study 1, the small telescopes approach was used to determine the SESOI, and the dual task results of Brünken et al. (2004) were used as group parameters. The sensitivity analysis indicated that an effect size of at least f = .28 (i.e., η_p^2 = 0.07) was required to yield meaningful results.

3.3.1.2 *Tasks Description and Materials*

PRIMARY TASK. The two finger-tapping tasks were the same as in Study 1. The synchronisation beeps indicated ISIs of either 300, 500, 700, 900, or 1100 ms.

SECONDARY TASK. The secondary task employed in the present study entailed detection of a simple auditory stimulus (duration = 80 ms; sound frequency = 220 Hz). The participant was required to press a response button with their left hand as soon as the reaction time beep was heard. These beeps were presented to the participant six times within a trial, at random moments. Reaction time beeps could not appear during the first six or the last three taps of a trial. Two successive beeps were spaced by at least two taps. As in Study 1, auditory stimuli were generated using MATLAB 7.11.0 R2010 software (Mathworks Inc.; Natick, Massachusetts, MA).

3.3.1.3 *Procedure*

Before commencing the experimental session, three simple reaction time measurements were taken from each participant. Then, a within-subjects design was applied, wherein each finger-tapping task was presented in a fully counterbalanced order.

For each of the two finger-tapping tasks, ISIs were randomly presented to the participant. A trial consisted in 60 synchronisation beeps. Overall, participants performed a total of 10 trials. The total duration of the experimental test period was ~40 min. Participants were debriefed at the end of the experimental session.

3.3.1.4 *Data Acquisition and Processing*

3.1.4.1 ACCURACY INDICATORS. To confirm that participants performed the finger-tapping tasks accurately, timing and spatial errors were computed. Before calculating accuracy indicators, the series of taps was checked to detect and remove data associated with IRIs greater than twice the ISI of a given trial. Having followed this criterion, 0.5% of the data were not retained for analytical purposes. Data in this category were referred to as temporal omissions. As in Study 1, relative asynchrony (ms) and spatial error (pixels) were used as indicators of synchronisation and spatial accuracy, respectively.

3.1.4.2 PRESSURE. Pressure was estimated by the deviation matrix of the touchscreen (surface acoustic wave technology) that was coded between -32768 and 32768.

Measured values were normalised on a scale ranging from 0 (no pressure) to 1 for the purpose of estimating the quantity of finger force applied on the touchscreen in the different experimental conditions.

3.1.4.3 SECONDARY TASK PERFORMANCE. The shortest of the three reaction times (RTs) measured prior to the experimental test session was taken as the reference value for a participant. For the RTs performed under dual-task condition, ΔRTs were computed as the percentage of the reference reaction time. As an example, if the reference RT was 200 ms and the dual-task RT was 250 ms, ΔRT was 125%. A key benefit of this delta method is to suitably compare the reaction-time increase between participants, ignoring inter-individual variability. Before calculating the ΔRTs, RTs three times as long as the reference reaction time were removed. Overall, 3.4% of the data were rejected on this basis. Finally, the mean $\bar{\Delta}$RT was computed over a trial and used as an indicator of the attentional demands required to perform the task.

3.3.1.5 *Statistical Analysis*

To monitor participants' performances in the two visuomotor tasks, the absolute asynchrony, spatial error, and pressure were submitted to a twoway RM ANOVA (Task [1 target, 6 targets] × ISI [300, 500, 700, 900, 1100 ms]). To examine H_3 and H_4, the $\bar{\Delta}$RTs were also submitted to a twoway RM ANOVA. Normality (Shapiro–Wilk test) and sphericity (Mauchly's test) were checked. Tukey post hoc tests were used as necessary. Statistica (v.13.1) was used for the statistical analyses, with alpha set at $p < .05$.

3.3.2 *Results*

3.3.2.1 *Descriptive Results*

Mean absolute asynchronies and spatial errors are presented in Table 2. To confirm that synchronisation and spatial accuracies were consistent with the findings reported in Study 1, an additional ANOVA was run with experiment (Study 1 vs. Study 2) as a between-subjects factor. The effect of experiment was non-significant for both the asynchrony, $F(1, 48) = 0.25$, $p = .622$, $\eta_p^2 = .054$, and spatial error, $F(1, 48) = 2.75$, $p = .104$, $\eta_p^2 = .005$.

Table 2
Synchronisation and Spatial Indicators for Study 2

Indicator	One-target pattern					Six-target pattern				
	300 ms	500 ms	700 ms	900 ms	1100 ms	300 ms	500 ms	700 ms	900 ms	1100 ms
Relative asynchrony	141	116	93	93	75	152	148	137	117	106
Spatial error	10.5	9.0	9.0	9.1	8.8	16.2	11.7	10.3	8.9	8.7

Note. Relative asynchrony (ms) and spatial error (pixel) for each inter-stimuli interval and each task.

SYNCHRONISATION ACCURACY. The RM ANOVA indicated a significant main effect of ISI, $F(4, 96) = 9.97$, $p < .001$, $\eta_p^2 = .29$, with the relative asynchrony decreasing steadily from the 300 ms ISI ($M = 147$, $SD = 61$) to the 1100 ms ISI ($M = 90$, $SD = 58$). The main effect of task was also significant, $F(1, 24) = 22.06$, $p < .001$, $\eta_p^2 = .48$, with a smaller relative asynchrony in the one-target ($M = 104$, $SD = 67$) vs. six-target condition ($M = 132$, $SD = 80$). The ISI $\times$ Task interaction was non-significant. Overall, these results indicated that participants made fewer timing errors as the tempo slowed down and when the motor task was easy.

SPATIAL ACCURACY. The RM ANOVA indicated a significant main effect of ISI, $F(4, 92) = 38.64$, $p < .001$, $\eta_p^2 = .63$, with more spatial errors in the 300 ms ISI ($M = 13.3$, $SD = 4.8$) vs. 500, 700, 900, and 1100 ms ISI conditions ($M = 9.5$, $SD = 3.1$). The main effect of task was also significant, $F(1, 23) = 10.91$, $p < .001$, $\eta_p^2 = .32$, with smaller spatial errors in the one-target ($M = 9.3$, $SD = 3.8$) vs. six-target condition ($M = 11.2$, $SD = 3.1$). The ISI $\times$ Task interaction was significant, $F(4, 92) = 12.30$, $p < .001$, $\eta_p^2 = .35$. This interaction reflected that spatial errors were smaller in the one-target vs. six-target condition, but only at the 300 ms ($p < .001$) and 450 ms ISI conditions ($p < .001$). Nonetheless, spatial errors were similar in other ISI conditions. Overall, these results confirmed that the participants made more spatial errors when the motor task was complex, and particularly so under high-speed execution (i.e., < SMT).

3.3.2.2 *Pressure*

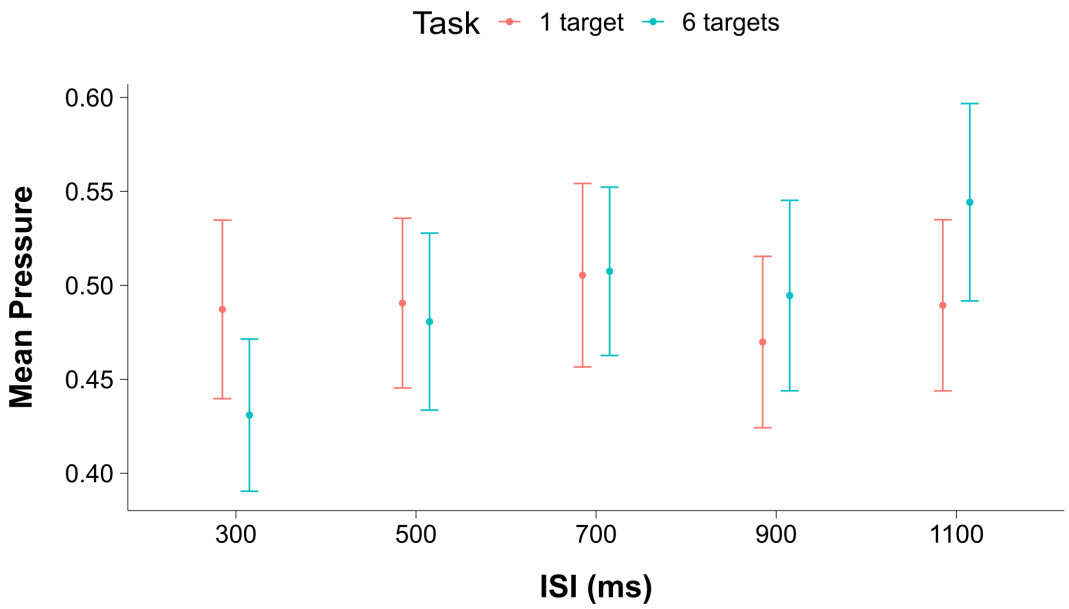
The RM ANOVA did not indicate any significant main effects of ISI or task. The ISI $\times$ Task interaction was significant, $F(4, 96) = 3.37$, $p = .019$, $\eta_p^2 = 0.12$. This interaction reflected that pressure was smaller in the six-target ($M = .43$, $SD = .20$) vs. one-target condition ($M = .49$, $SD = .24$) in the 300 ms ISI condition ($p = .014$). Nonetheless, the pressure was greater in the six-target ($M = .54$, $SD = .26$) vs. one-target condition ($M = .49$, $SD = .23$) in the 1100 ms ISI condition ($p = .017$). Overall, these results indicated that the participants modulated the pressure applied to perform the task only in the six-target condition (Figure 9).

3.3.2.3 *Secondary Task Performance*

The $\bar{\Delta}$RTs were first tested against 100 with paired-samples t tests. To account for multiple comparisons, p values were Bonferroni-corrected at $p = .05/10 = .005$. All comparisons were statistically significant ($p < .001$).

The RM ANOVA conducted on the $\bar{\Delta}$RTs indicated a main effect of ISI, $F(4, 96) = 7.33$, $p < .001$, $\eta_p^2 = .23$, with shorter $\bar{\Delta}$RTs in the 300 and 500 ms ($M = 165.14$, $SD = 34.45$) vs. 900 and 1100 ms ISI conditions ($M = 177.07$, $SD = 36.67$). The main effect of task was also significant, $F(1, 24) = 44.38$, $p < .001$, $\eta_p^2 = .65$, with smaller $\bar{\Delta}$RTs in the one-target ($M = 164.22$, $SD = 31.89$) vs. six-target condition ($M = 177.30$, $SD = 38.40$). The ISI $\times$ Task interaction was significant, $F(4, 96) = 9.27$, $p < .001$, $\eta_p^2 = 0.29$. This interaction reflected the fact that $\bar{\Delta}$RTs were smaller in the one-target vs. six-target condition, but only for the 300 ($p < .001$), 500 ($p = .008$), and 1100 ms ISI tempi ($p = .004$; Figure 10). Note that the effect sizes of both the main effects and the interaction

Figure 9
Pressure Results for Each Experimental Condition



Note. Mean pressure for each inter-stimuli interval, and each task. Errors bars represent 95% confidence intervals. ISI = inter-stimuli interval.

were greater than the required SESOI, which indicated that the effects were large enough to be considered meaningful.

3.3.3 *Discussion*

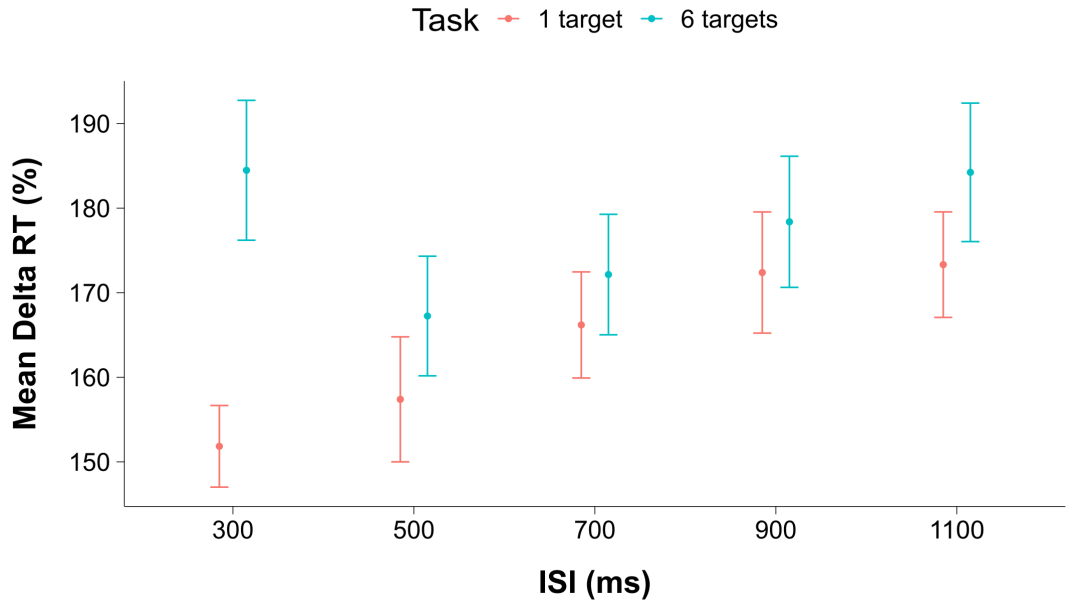
The general aim of Study 2 was to examine the attentional demands of sequential movements performed at various paces by means of a dual-task paradigm. Both timing and spatial errors were similar to those presented in Study 1 and previously reported in the literature using finger-tapping tasks during SMS (Dione & Delevoye-Turrell, 2015). These findings indicated that participants were able to perform the dual task without decreasing their performance in the primary task.

The findings of Study 2 demonstrated that motor production was always associated with a significant cognitive cost. The ACs were indeed systematically greater in dual than single tasking ($\bar{\Delta}$RTs > 100). Tapping is a spontaneous movement that is sometimes observed in individuals who do not even realise that they are moving. The present findings are of interest for education because they indicate that suppressing this spontaneous body movement could help young adults gain concentration by freeing cognitive resources (Nadeau & Rousseau, 1986).

Results of Study 2 highlighted an effect of task complexity, with finger tapping in the complex conditions (six-target trials) engaging more attentional resources than finger tapping in the simple conditions (one-target trials). When the tapping was directed to a visual pattern of six targets, participants needed to control their pointing actions both through time and space. These requirements were in clear-cut contrast

Figure 10

Reaction Time for Each Experimental Condition



Note. Mean ΔRTs for each inter-stimuli interval, and each task. Errors bars represent 95% confidence intervals. RT = reaction time; ISI = inter-stimuli interval.

with that needed in the one-target task, for which a simple one-joint movement of the finger was required, up-down in time with the external metronome. Figure 10 illustrates that for the one-target trials, the cognitive load increased proportionally with the decrease in tempo.

For the six-target trials, the attentional demands were important at both extremes, with a minimum around the SMT. This contrasting pattern is probably related to the fact that the six-target trials required greater motor planning, preparation, and online control than the one-target trials (see Paillard, 1985). Hence, motor-timing strategies were adapted to compensate for motor-task complexity. In the slow trials, attention was needed to maintain concentration on the task and manage slow body movements with both temporal and spatial constraints. In the fast trials, attention was required to move the limb fast enough through space. The easiest pace was experienced at SMT for which both time and space were controllable with optimal sensorimotor loops.

Performing slow movements required cognitive resources. In both simple (one-target trials) and complex (six-target trials) finger-tapping tasks, the cognitive load of motor execution was more important when moving slow vs. fast. The results of Study 1 indicated that finger tapping at slower tempi was characterised by more negative ACs than finger tapping at faster tempi. This pattern of results suggests that slow voluntary actions were performed in the predictive timing mode. Thus, greater cognitive control was necessary for each tap in the motor sequence.

Findings of Study 2 support this hypothesis by indicating that the slower the tempo, the more cognitive resources are needed. At the slowest tempo (i.e., 1100 ms

of ISI), cognitive control led to an increase in muscle co-contraction that was quantifiable by a significant increase in the finger pressure on the screen. Overall, these results may reflect that attention is used to inhibit the urge to move spontaneously faster. This interpretation is consistent with the proposed involvement of executive functions when decreasing the pace of voluntary movement (Provasi & Bobin-Bègue, 2003).

When moving at fast tempi, the attentional resources needed to produce a voluntary movement varied depending on task complexity. In the one-target trials, a single-joint movement of the finger was sufficient to perform the task. Hence, correct performance was reached by creating a rigid body (finger, wrist, shoulder) with a single degree of freedom around the elbow. Accordingly, the central cognitive system did not need to regulate multiple articulations through space. Finger pressure remained consistent across tempi, indicating that a similar biomechanical system was involved.

To perform the six-target trials, each participant needed to coordinate muscle contractions of upper limbs through time and space. This required the implementation of online corrective mechanisms. In slow trials, individuals had time to co-contract upper limbs to achieve superior control in terms of spatial accuracy. The co-contraction led to an increase in finger pressure on the screen.

In the fast trials, the burden of motor complexity on the attentional reservoir led individuals to change their timing strategy to prioritise space over time. This was visible in the fastest trials (i.e., 300 ms of ISI), for which participants started to reach the biomechanical limits of the sensorimotor-control loops. Attention was absorbed in moving the hand through space to execute the finger-tapping task as best as possible. Limb displacements were facilitated by less co-contractions of upper limbs (i.e., loosening of the articulations), which led to a significant decrease in finger pressure on the screen.

3.4 GENERAL DISCUSSION

Over two decades, researchers in neuroimaging have argued that there is differential control in emergent and predictive timing (for reviews, see Buhusi & Meck, 2005; Wiener et al., 2010b). The processing of slow durations (i.e., sub-second intervals) were found to activate prefrontal regions while fast durations (i.e., supra-seconds intervals) preferentially activate motor and premotor areas (Lewis & Miall, 2003b; Lewis & Miall, 2003c). Yet, these *f*MRI studies failed to promote an explanatory hypothesis for the existence of a dual-timing strategy; actually, they merely reported differences in brain activation patterns according to interval duration in perceptual discrimination tasks. In this chapter, a particular emphasis was placed on testing the nature of the cognitive process that are involved in the production of time intervals. Specifically, I adapted mathematical tools and the classic dual-task paradigm to shed light on the cognitive aspects of motor timing for tempi ranging from 300 to 1100 ms of ISI.

3.4.1 *A Dynamic Process*

In the present chapter, motor tasks were specifically designed to reflect contrasting complexity similar to that found in real-life situations. Most people have experienced the pleasure of eating popcorn while watching a film. Moving the hand from the bucket to the mouth is easy and allows the movie-goer to enjoy the snack while being immersed in the on-screen action. Eating a hot bowl of soup, however, is another matter. Here, one must control the trajectory of the hand to lead the spoon to the mouth without spilling. Such movement is performed more slowly and with much more attention. Under these circumstances, it is rather hard to do something else concurrently. There is greater attentional resources demanded by the nature of the movement. These examples illustrate how the allocation of attentional resources is adapted in everyday activities in response to constraints imposed by the environment on the motor system (see also Jones et al., 2002).

Using a behavioural task, the dynamic alternation between emergent and predictive timing under different timing and spatial constraints was examined. Two key results surfaced from the data. First, the ACs were always negative. This observation can be explained by the fact that sequential pointing is a discrete task by nature. Nevertheless, ACs were found to be more or less negative depending on the externally-imposed tempo. At slower tempi, the times series was found to be strongly negative, which suggests that online control entailed a significant cognitive cost. Here, participants had sufficient time to prepare and correct each individual pointing movement. By contrast, at faster tempi, the time series was found to be less negative, which indicates that the action was executed with a need for fewer attentional resources. In such conditions, there was less online control due to temporal pressure. Hence, moving either slow or fast yielded two contrasting patterns of behavioural results.

When an action is simple (e.g., pointing to a single point in space), the same motor command can be triggered without adjustments, as similar muscle coordination can be repeated over time. Individuals only need to manage the action temporally, to decide when to trigger the release of the motor command. This way, the regulation of movements is automatic (Maes et al., 2015) and requires little cognitive control (Delevoye-Turrell et al., 2006). Thus, motor actions are performed without the need for online feedback (i.e., open motor loop; Seidler et al., 2004). Nonetheless, even in such a simple scenario, individuals need to resist the urge to move in accord with their SMT when producing slow movements. As a consequence, a mental representation of the timing properties of the ongoing action is needed (for a review of temporal–predictive processes, see Schwartze et al., 2012).

Benefiting from an explicit representation of time, predictive timing allows for a cognitive monitoring of action performance. In particular, this might imply the processing of the sensorimotor flow of information, working memory, and attention (Berret & Jean, 2016; Krampe et al., 2010). These processes are part of high-level cognitive control processes that are demanding in terms of resources. When such cognitive control is lacking, inadequate behaviours can be observed, as those found in impulsive disorders (see Grisetto et al., 2019; Wittmann et al., 2011). In the experimental studies of this chapter, participants possessed the capacity to inhibit the

urge to move at a significant cognitive cost. Indeed, under dual-task conditions, the reaction times were slower in the slow vs. fast and close-to-SMT trials .

When an action is complex (e.g., an individual is required to point at different locations), individuals must deal with both time and space constraints. Pre-planning is not sufficient as the trajectory of each element will need to be adapted as a function of the errors that manifest in the previous element of the sequence. Hence, motor performances will take advantage of online corrections, which are implemented through sensorimotor re-afferences that inform the central-cognitive system of performance errors. In the present chapter, the finger-tapping task in the six-target trials needed to be spatially regulated. Hence, movement execution relied on the visuo-motor feedback loops to maintain performance accuracy.

3.4.2 *Critical Role of Available Attentional Resources*

Generating a corrective signal for the motor commands is the outcome of the comparison between what is wanted (i.e., efference copy), and what was actually done (i.e., sensorimotor reafferences; Bard et al., 1992). Consequently, sensory afferences need to be processed and compared to the information stored in working memory to update the motor commands. When moving slow, the system has the time to extract information from the control loops and implement corrections on each and every element of the sequence to minimise spatial and timing errors.

During the production of fast movements, the system does not have sufficient time to feed the motor loops in order to detect and correct errors – which is detrimental to efficient movement realisation. This is evidenced by the greater number of temporal and spatial errors. Because reaching the limits of the control loops, the motor peripheral system takes over at fastest tempi in the six-target trials. The cognitive cost of motor control remained high, but was associated with a release of (a) degrees of freedom in the upper limbs and (b) predictive timing mechanism. An explicit representation of time was no longer used to guide motor timing, but the temporal properties emerged directly from the dynamics of the body in motion.

When the available attentional resources are sufficient to execute the motor plan and maintain the performance level, cognitive control of movement execution is feasible. However, when movement complexity and time pressure are too important, cognitive control and the degrees of freedom of motor control are adjusted to simplify motor execution and preserve timing accuracy. This motor-control simplification is further corroborated by the pressure force applied to perform the task. An increase in motor compliance – corresponding to a decrease in muscular tone – was found when movement complexity and time pressure were high.

It is possible that limb-control simplification entails a drop in the energy required to perform the movement. Indeed, individuals have a natural tendency to achieve the most cost-effective behaviour (Selinger et al., 2015). An implication of the energetic cost-minimisation framework is that energy cost continuously shapes movement (Cheval et al., 2018a). Thus, individuals constantly pursue a good balance between cognitive cost and efficiency. This fundamental principle is why there is sometimes a mismatch between "how well an organism can potentially perform, and how well that organism actually performs on a given task" (Inzlicht et al., 2018,

p. 338). In the present chapter, I reported data from two studies that confirm the idea that timing properties emerge from body oscillations when the cognitive cost of motor control is too high due to movement complexity and/or time constraints. When difficulty arises, the biological system adopts the strategy to minimise the cognitive cost of moving by focusing on the *where* and letting body dynamics take charge of the *when*.

3.4.3 *Limitations*

There are two main limitations in the present contribution. First, different ISI conditions were used in Study 1 and 2. The decision to change the tempo conditions was taken because following Study 1, I felt that the time span between the fastest and the slowest conditions was insufficient – only the 1000 ms ISI induced significantly more negative asychronies when compared to the 300 ms ISI. Hence, a slower tempo condition (i.e., > 1 s) was introduced in Study 2, while keeping the same number of ISI to limit fatigue. Second, the design of Study 2 did not include a single-task condition. This choice was made to constrain the experimental session duration but limited a truly meaningful between-experiment comparison. Future studies should target the inclusion of single-task control in a dual-task paradigm where possible, and might use an ISI condition that matches each participant's spontaneous motor tempo to allow for inter-individual differences.

3.4.4 *Conclusions*

The findings of the present chapter highlighted the significance of crossing mathematical and psychological tools to offer a holistic view of the cognitive processes involved in motor timing. Findings suggest that emergent and predictive timing are underpinned by distinct mechanisms that are characterised by different levels of cognitive control (see also Holm et al., 2017). Slow movements appeared to be more prone to cognitive monitoring (i.e., predictive timing), whereas fast movements were characterised by a release in control (i.e., emergent timing). The introduction of a "cognitive control into the rigid machinery of sensorimotor habits" (Paillard, 1991, p. 248) takes time. The more time an individual has, the more a movement can be performed, controlled, and corrected under the cognitive wings of predictive timing.

INTERMEDIATE SUMMARY

Human beings adjust the spontaneous pace of their actions to interact with their environment. Yet, the nature of the mechanism enabling such adaptive behaviour remains poorly understood. The aim of Chapter 3 was to examine the role of cognitive control in motor timing using (a) time series analysis and (b) a dual-task paradigm. In a series of two studies, a finger-tapping task was used in SMS with various tempi (from 300 to 1100 ms) and motor complexity (one target vs. six targets).

Time series analyses indicated that two different timing strategies were used depending on the pacing constraints. At slow tempi, tapping sequences were characterised by strong negative autocorrelations, suggesting the implication of cognitive predictive timing. When moving at fast and close-to-SMT tempi, tapping sequences were characterised by less negative autocorrelations, suggesting that timing properties emerged from the body-movement dynamics. The analysis of the dual-task reaction times confirmed that the production of slow movements required more attentional resources than the production of fast movements. Overall, findings of Chapter 3 suggest that moving fast and slow involve distinct timing strategies that are characterised by contrasting attentional demands.

Chapter 3 has been published in *Frontiers in Psychology* (2021). In addition, the results have been the subject of one oral presentation (2019, 14e Journée Scientifiques des Jeunes Chercheurs, Lille, France) and one poster presentation (2019, 7th Mind-BrainBody Symposium, Berlin, Germany).

If the abilities to produce slow and fast movements are underpinned by distinct timing strategies, they should rely on separate brain structures. More precisely, the production of slow movement (i.e., predictive timing) should involve brain areas devoted to high-cognitive processes (e.g., dorsolateral prefrontal cortex; Gbadeyan et al., 2016; MacDonald et al., 2000). Conversely, fast-movement production (i.e., emergent timing) should entail brain areas engaged in body dynamics (e.g., primary motor cortex; Yokoi et al., 2018). The general aim of Chapter 4 was to highlight distinct patterns of brain activation during the production of fast and slow movements.

4

EFFECTS OF MOTOR TEMPO ON FRONTAL BRAIN ACTIVITY

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4.1 INTRODUCTION

The coding of time by the brain remains a mystery for the simple reason that there are no time-specific sensory receptors. Initial studies in neuropsychology referred to a normative scale depicted in the form of an internal clock. Conceptualised by Treisman (1963), the internal clock is described as a pacemaker-accumulator model that has become the most popular concept model to date (Droit-Volet & Wearden, 2003). It is composed of three distinct stages in which temporal information about an event is extracted, encoded, and processed. However, the internal clock metaphor was primarily created to fulfil the need of a conceptual framework, and is now challenged by biological and pharmacological research, which suggests that time may be embedded within the neural activity of the cortex (Buhusi & Meck, 2005).

Since the turn of the millennium, neuroscientific studies have indicated that specific brain structures may play a function in time processing; notably the cerebellum and the basal ganglia, with wider networks including the supplementary motor area, the prefrontal cortex, and the posterior parietal cortex (Buhusi & Meck, 2005; Ivry & Spencer, 2004; Rubia & Smith, 2004). However, a major limitation in the literature is the fact that most of the neuroimaging studies have focused on the perception of time, while neglecting the question of motor timing (Bareš et al., 2019; Grahn & Brett, 2007; Jongsma et al., 2007). Although previous findings have indicated that the brain areas dedicated to time perception are similar to those devoted to time production (Rubia & Smith, 2004; Schubotz et al., 2000), due care should be taken in generalising such results given that these studies were conducted by use of *f*MRI. It is extremely difficult to execute studies with motor paradigms using *f*MRI, as this technology is highly sensitive to movement artefacts.

Over the last decade, the noninvasive imaging method of *f*NIRS has become the tool of choice for those investigating motor paradigms (Leff et al., 2011). It makes use of the optical proprieties of light in order to evaluate local hemodynamic responses (i.e., increase in blood flow) in a given cortical area. Notably, the brain is one of the body parts in which the metabolic activity is most intense (up to 20% of energy consumption of the body at rest; Attwell et al., 2010; Gusnard & Raichle, 2001) and yet it possesses no reserves of energy. Hence, the brain has developed a large vascular network that can perpetually support its nutritional requirements. The local electrical activity of the neurons (i.e., action potential) engenders an energy cost in oxygen and glucose, that is met by metabolically active cells (i.e., astrocytes; Magistretti et al., 1999). This provides the resources for effective cerebral activity (León-Carrión &

León-Domínguez, 2012). *f*NIRS is a neuroimaging technique that provides a means by which to assess such changes in brain metabolism, and thus allows the researcher to infer related neural activity.

Near-infrared spectrum light uses the optical window in which the diffusion of light through biological tissues is the greatest. It is notable that skin, tissue, and bone are mostly transparent to NIR light in the optimal spectrum of 700–900 nm, while HbO_2 and HHb are stronger absorbers of light. Thus, differences in the absorption spectra of HHb and HbO_2 allow the calculation of the relative changes in haemoglobin concentration through the use of the degree of light attenuation at multiple wavelengths (Strangman et al., 2002). Consequently, *f*NIRS can provide specific information on brain oxygenation (i.e., HbO_2), deoxygenation (i.e., HHb), and the total content of haemoglobin (i.e., HbT). In the present study, the *f*NIRS technique was used to measure changes in oxygenation of the brain tissues over the prefrontal and motor areas. This enabled a fuller understanding of the relative contributions of these brain areas to motor timing.

The behavioural task that is most commonly used to study motor timing in experimental psychology is the tapping paradigm (Repp, 2005). Early studies measured the spontaneous tapping speed of the hand – referred to as the *spontaneous motor tempo* – to further understand people's "natural pace" (Fraisse, 1982; Fraisse et al., 1954). Among the general population, this idiosyncratic tempo is subject to considerable interindividual variability (Drake & Baruch, 1995; Fraisse, 1974); nevertheless, spontaneous motor tempo is found to average ~2 Hz (i.e., 500-ms time intervals; McAuley et al., 2006; Moelants, 2002). *f*NIRS has been used in self-paced finger-tapping paradigms (Drenckhahn et al., 2015; Holper et al., 2009; Sato et al., 2007; Wilson et al., 2014). Results have shown that brain hemodynamic responses depend on task complexity, with complex tasks (e.g., bimanual tapping) eliciting significantly larger HbO_2 changes in the premotor area and the primary motor cortex than simple unimanual tapping (Holper et al., 2009). Nonetheless, few studies have used *f*NIRS techniques to ascertain how the brain modulates the spontaneous motor tempo.

Humans live in a constantly changing and evolving environment. Hence, adapted behaviours require individuals to be able to accelerate or decelerate the spontaneous pace of their own motor actions to facilitate smooth interaction with individuals and objects present in their environment (Bryant & Barrett, 2007). Such motor timing abilities are commonly assessed using SMS tasks. In fact, this approach concerns "a form of referential behaviour in which an action is temporally coordinated with a predictable external event, the referent" (Repp, 2005, p. 969). SMS tasks have shown that the ability to adapt the timing of voluntary actions to environmental constraints develops with age as well as experience. For example, babies are unable to alter the speed of their natural behaviours. When required to synchronise self-generated actions to slow auditory stimuli, newborns and 2-month-old babies were reported to be unable to slow down their non-nutritive sucking rate below their spontaneous motor tempo (Bobin-Bègue et al., 2006). Similar results were found in 3½-year-olds during the synchronisation of hand-tapping with slow auditory and visual stimuli (Bobin-Bègue & Provasi, 2008). Bobin-Bègue et al. (2006) suggested that the ability to slow down movements depends on motor inhibition, a process that is a component

of high-level cognitive functions. Thus, it would only be acquired later in ontogeny and have functional impact from 8 years and beyond (Williams et al., 1999).

If the ability to modulate motor tempo according to the environmental constraints is underpinned by cognitive functions, it should involve frontal activations. Following this train of thought, Kuboyama, Nabetani, Shibuya, Machida, and Ogaki (2004, 2005) reported a gradation in cerebral oxygenation of the motor cortex in accord with the frequency at which a finger-tapping task was performed. Larger hemodynamic responses were found for maximal speed tapping compared to slower tapping conditions. However, neither of these studies investigated prefrontal activations as a concomitant of the pace of motor execution.

The main objective of the present study was to examine the cerebral oxygenation of prefrontal and motor areas simultaneously during the execution of visuomotor tasks performed under different time constraints. Three forms of upper-limb movement were used to control for motor complexity and facilitate generalisation of the findings: A simple task (i.e., finger-tapping task, discrete movements with a recognisable beginning and end), a task of moderate complexity (i.e., pointing task, serial individual-movements linked together to constitute a whole), and a complex task (i.e., circle drawing task, continuous movements with no recognisable beginning and end; Schmidt et al., 1988). These three SMS tasks were administered via a computer touchscreen according to three externally-paced tempi: fast pace (i.e., 300 ms), natural pace (i.e., 500 ms), and slow pace (i.e., 1200 ms).

To ensure methodological rigour, acquisition and filtering pipelines, as well as raw data, were reported (Leff et al., 2011). To discriminate between physiological noise and cerebral meaningful signals, the physiological data (i.e., heart and respiratory rates) were recorded throughout the experimental session so that frequency bands of such signals could be regressed from the *f*NIRS data. An automatic tracking of the headset was also used to monitor the exact position of the optodes in reference to the cranio-cerebral correlates of the NIR channels.

Motor timing at the spontaneous motor tempo would lead to less prefrontal (i.e., anterior and dorsolateral prefrontal cortices) and motor (i.e., premotor and primary motor cortex) activation when compared to performing the motor task at either fast or slow tempi (H_1). Furthermore, action production at slow tempi would lead to a significantly greater increase in cerebral oxygenation over the prefrontal lobe when compared to task execution at a fast tempo, for which the increase in cerebral oxygenation would involve motor areas (H_2). Similar patterns of activation would be observed regardless of the complexity of the motor task being undertaken (H_3).

4.2 METHODS

4.2.1 *Participants*

Healthy adults were recruited for the present study from among the corpus of University of Lille staff and students. Participants were right-handed (assessed by use of the Edinburgh Handedness Inventory; Oldfield, 1971), had normal to corrected-to-normal vision, and did not present motor dysfunction or neurological/psychiatric disorders. A pilot test conducted on two participants confirmed that both hair den-

Table 3
Estimated Required Sample Size and Critical Statistical Tests

Hypotheses	Groups	Measurements	Planned analysis	Critical statistical tests	Required sample size	SESOI
H_1	9	2	RM MANOVA	Contrast 1: 500 ms vs. 300 ms Contrast 2: 500 ms vs. 1200 ms	15	.22
H_2	9	2	RM MANOVA	300 ms vs. 1200 ms	16	.22
H_3	9	2	TOST	Simple vs. moderate task Simple vs. complex task Moderate vs. complex task	16	.62

Note. Statistical power, planned analyses, and critical statistical tests for each research hypothesis. SESOI = smallest effect size of interest (d_z); RM ANOVA = repeated-measures analysis of variance; TOSTs = two one-sided tests.

sity and length could induce significant noise in *f*NIRS data (Figure 3). Ongoing work in our laboratory is targeting potential solutions to address this limitation that pertains to *f*NIRS technology. Nevertheless, for the present study, only male participants with very short haircuts (< 1 cm) or shaven heads were included to avoid hair-related issues (McIntosh et al., 2010; Pringle et al., 1999). Participants were informed of the tasks to be performed and the measurements to be taken at least 48 hr prior to their participation. After reading an information sheet, each participant was invited to provide written informed consent. At this point, demographic data were collected (sex, age, and musical expertise). The ethics committee of the University of Lille (France) approved the study (see Appendix A).

The sample size required for the critical statistical test of each research hypothesis was calculated using G*Power (3.1.9.2; see Table 3). For H_1, H_2, and H_3, the *f*NIRS results of Abiru et al. (2016) were used as group parameters. For H_1 and H_2, Tukey post hoc tests were the critical statistical tests. Because a Tukey test is essentially a modified t statistic that corrects for multiple comparisons, required sample size was also computed for paired-samples t tests. The power analysis indicated that 15 participants would be required for H_1 (d_z = .68; α = .05; 1-β = .80), and 16 participants for H_2 (d_z = .67; α = .05; 1-β = .80). For H_3, required sample size was also computed for paired-samples t tests. The power analysis indicated that 16 participants would be required (d_z = .67; α = .05; 1-β = .80). Accordingly, a sample of 16 participants was recruited.

The small telescopes approach was used to determine the SESOI (i.e., the difference that is considered too small to be meaningful; Simonsohn, 2015) for each hypothesis. Accordingly, the SESOI was set to the effect size that an earlier study would have had 33% power to detect (Lakens et al., 2018). As previously, the *f*NIRS results of Abiru et al. (2016) were used for H_1 and H_2. The *f*NIRS results of Miyai et al. (2001) were used for H_3. The SESOI for each hypothesis is reported in Table 3.

4.2.2 *Experimental Procedure and Tasks*

4.2.2.1 *Experimental Procedure*

Each participant was administered three visuomotor tasks via a touchscreen on which he used his right index finger, with a closed fist. An *f*NIRS headset was worn by the participant throughout the session. The touchscreen (1915L Elo Touch 19"; Elo Touch Solutions Inc.; Milpitas, California, CA) was placed on a table in front of the participant with the screen oriented at 45°. The participant was seated on a stool, suitably adjusted to her/his height to minimise lower-limb muscular fatigue (assessed by use of the rating-of-fatigue scale; Micklewright et al., 2017) and avoid any extraneous movements during task performance. The stool was fixed in such a way that horizontal rotational movement would be possible. The experimental session took place in a quiet, windowless room that was dimly lit. The lighting is of particular importance given that bright light can affect *f*NIRS signals (Shadgan et al., 2010). The *f*NIRS system (FOIRE-3000/16; Shimadzu, Kyoto, Japan) was placed behind the participant to limit distraction and facilitate the management of the cables. This setup also provided a means by which to minimise the weight of cables on the participant's neck. To verify that this was effective, a self-rated pain scale of was administered. The scale was attached to a 9-point Likert scale, ranging from 1 (*no pain*) to 9 (*unbearable pain*). The participant was required to indicate the degree of pain that he was experiencing in regard to the weight of optodes on the head and neck. This pain scale was presented at the beginning of each block of trials as well as at the end of the experiment, for an overall evaluation of the participant's experience.

4.2.2.2 *Task Description*

A total of three visuomotor tasks were administered in a counterbalanced order across participants. In the finger-tapping task, the participant was required to tap on a single visual target (dot of 10-mm diameter) located in the centre of the touchscreen (Figure 11, left panel). In the pointing task, six targets (dots of 10-mm diameter) positioned around an invisible circle of 100 mm radius were displayed on the screen. The participant was asked to tap each target, one after the other (Figure 11, middle panel). In the drawing task, six targets of a similar nature linked together to form a 100-mm circle were displayed on the screen (Figure 11, right panel). The participant was required to trace the circle and, in so doing, produce a regular and continuous arm movement. In both the pointing and the drawing tasks, the participant was instructed to start with the finger above the top-right target and move counterclockwise. The participant was instructed to maintain accuracy in both temporal and spatial facets of the skill, but to favour temporal accuracy in case the task became too challenging for both to be maintained.

The participant performed the tapping, pointing, and drawing tasks at three predefined tempi that were set by an auditory metronome. The beeps of the metronome had a duration of 80 ms and a sound frequency of 294 Hz. The beeps were generated using Matlab 7.11.0 R2010 software (Mathworks Inc.; Natick, Massachusetts, MA).

The three tempi used in the study were 300 (for the fast-tempo trials), 500 (for the natural-tempo trials), and 1200 ms (for the slow-tempo trials). For the fast- and

slow-tempo trials, this enabled the participant to depart from her/his spontaneous motor tempo but remain within the possible SMS zone (between 180 and 1800 ms, Keele et al., 1985; Mates et al., 1994). These metronome tempi were played to the participant via two Creative SBS 250 desk speakers (Creative Technology; Singapore) positioned either side of the screen.

4.2.2.3 *Experimental Design*

The experiment was predicated on a block design procedure, characterised by alternating periods of activity and respite to facilitate the acquisition of reliable *f*NIRS signals (Gervain et al., 2011). It has been shown that the best *f*NIRS signal is obtained with a resting period of 30 s prior to stimulation (Obrig et al., 1997). Accordingly, each 60-s trial was preceded by a rest period of 30 s to allow the hemodynamic indices to return to their baseline levels and to optimise the quality of the hemodynamic responses to time-locked body movements.

The participant performed a series of 12 blocks, for a total of 36 trials. In a first series, the participant performed the three visuomotor tasks in a randomised order at a self-paced spontaneous tempo (i.e., executed at a regular and most natural pace). In a second series, he performed the three visuomotor tasks while synchronising their movements to the metronome. Three blocks of trials were recorded for each task, with the slower, natural, and faster conditions administered in a random order.

Throughout the session, the participant was instructed to leave his left arm hanging by their side in a relaxed manner. The participant was also informed not to speak and to avoid extraneous movements during each *f*NIRS trial. The self-paced trials were systematically administered before the externally-paced trials to avoid cross-contamination (Bove et al., 2009). The total duration of the experimental test period was ~100 min.

4.2.3 *Data Acquisition and Preprocessing Analyses*

4.2.3.1 *Behavioural Data Acquisition and Preprocessing*

In the tapping and pointing tasks, IRIs were measured as the time interval between the onset of successive taps. In the drawing task, radii from the centre of the circle to each target were computed first. Taps were defined as the locus that intersected the participant's finger and each radius. Before conducting the main analyses, the time series were checked in order to detect and remove the IRIs greater than twice the ISI of the given block of trials. These trials were referred to as "temporal omissions" and were not included in the statistical analyses.

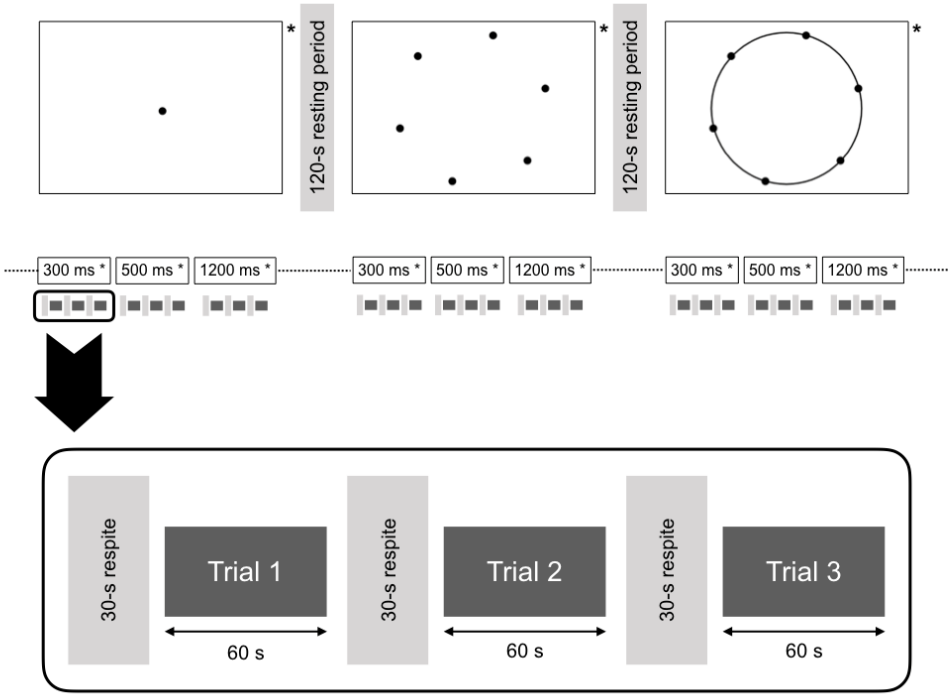
An IRI_{error} was computed as the percentage of absolute difference between an IRI and its reference ISI for a given time interval t (Equation 4).

$$IRI_{error(t)} = (|IRI_t - ISI|)/ISI \times 100 \quad (4)$$

The mean IRI_{error} measurement within a trial indicated the accuracy of time interval production (i.e., behavioural tempo-accuracy; Repp, 2005).

For each time interval t, a spatial error was computed (pixels), as the difference between the centre of the visual target and the location of the participant's forefinger.

Figure 11
Diagrammatic Representation of the Experimental Design for the Sensorimotor Synchronisation Conditions



Note. * = randomisation.

The mean pointing error within a trial was used as an indicator of behavioural-spatial accuracy (Dione & Delevoye-Turrell, 2015).

4.2.3.2 *f*NIRS Data Acquisition

Data were collected using a continuous-wave *f*NIRS system operating at three near-infrared wavelengths (780, 805, and 830 nm) and monitored by the associated Lab-NIRS software. This *f*NIRS system offers 32 optodes divided into 16 light sources (multicomponent glass bundle fibers) and 16 detectors (multi-alkali photomultipliers detectors). The sampling frequency was set at 2.27 Hz (i.e., temporal resolution of 440 ms).

The brain regions of interest were the prefrontal cortex (dorsolateral prefrontal cortex; Brodmann's area 9) and motor cortex (premotor and primary motor cortices; Brodmann's areas 4 and 6; Homan et al., 1987; Okamoto et al., 2004). Thus, a 45-channel (28 optodes, 45 source-detector couples) configuration was applied in order to cover these cortices over both brain hemispheres (Figure 12). One additional channel was applied to the occipital cortex (Brodmann's area 18) as a means of providing "negative control" (i.e., control an area of the brain not expected to be influenced by the experimental manipulations). The optodes were attached to a 32-optode headset with a 3-cm source-detector distance, giving a depth of analysis from 0.5–2.0 cm. The

headset was placed on each participant's head in accord with the International 10–20 system guidelines for standard electrode positions (Jasper, 1958). As a result, the Cz optode was located at the midway point between the nasion and inion.

System calibration was performed through an automatic adjustment using LabNIRS to adapt the internal parameters of the *f*NIRS device (e.g., gain, amount of light to emit) to the head morphology and the hair-type characteristics of each participant. Differences in the absorption of HbO_2 and HHb provided the means to measure the differences in the haemoglobin concentration (µmol/L). These differences were computed in real time using Equation 5 and 6 (generated by LabNIRS from the modified Beer-Lambert law; Baker et al., 2014):

$$\begin{aligned} HbO_2 = (\text{-}1.4887) \times \text{Abs}[780\text{nm}] + 0.5970 \times \text{Abs}[805\text{nm}] \\ + 1.4847 \times \text{Abs}[830\text{nm}] \end{aligned} \tag{5}$$

$$\begin{aligned} HHb = 1.8545 \times \text{Abs}[780\text{nm}] + (\text{-}0.2394) \times \text{Abs}[805\text{nm}] \\ + (\text{-}1.0947) \times \text{Abs}[830\text{nm}] \end{aligned} \tag{6}$$

The HbT will then be established through a summation of HbO_2 and HHb (Equation 7):

$$HbT = HbO_2 + HHb \tag{7}$$

4.2.3.3 *Preprocessing of fNIRS Data*

Data (HHb, HbO_2, and HbT) were first filtered to eliminate mechanical artefacts (quick baseline shifts of the signal waveform characterised by sharp and steep edges) and physiological noise (heart and respiratory rates). This enabled the research team to keep only the physiological hemodynamic signals X (HHb, HbO_2, and HbT), which show slow variations over time (Pinti et al., 2019). The precise preprocessing pipeline was defined in accord with the shape of the data, as there is presently no consensus in the *f*NIRS literature regarding filtering methods (Pinti et al., 2019).

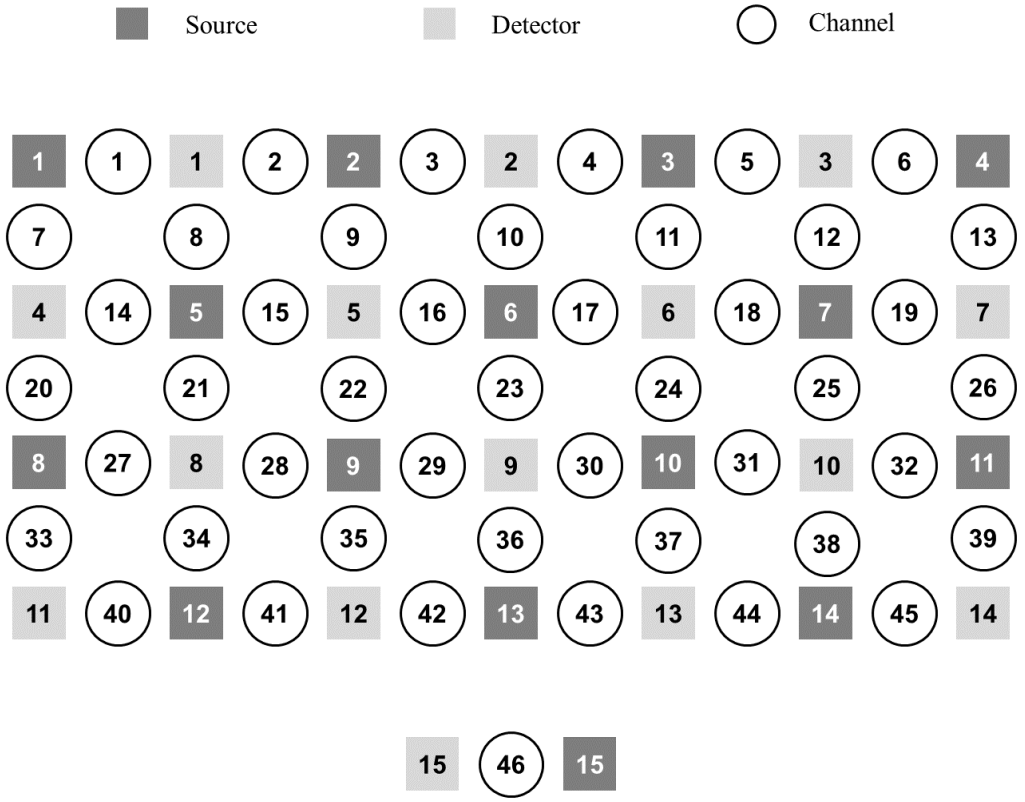
For each trial i, a baseline $B_{X,i}$ and a plateau $P_{X,i}$ were defined as the mean values of X upon a 5-s time window starting 10 s before the trial onset and upon the last 5 s of the trial, respectively (for similar calculations, see Mandrick, 2013). Then, the variations $\Delta_{X,i}$ of a trial were given relative to its baseline (i.e., by subtracting $B_{X,i}$ to $P_{X,i}$), to be free from possible offsets across trials and linear trends of the signal over time. The mean $\bar{\Delta}_{X,n}$ was computed over each block n, for each channel, in each condition (for similar calculations, see Derosière et al., 2014; Mandrick et al., 2013). Finally, the mean variations in HbO_2, HHb, and HbT were given for two channel clusters defined according to the two regions of interest: $\bar{\Delta}_{X,\,\text{prefrontal}}$ and $\bar{\Delta}_{X,\,\text{motor}}$.

4.2.3.4 *Controlling for Noisy Signals*

Data contamination caused by movement and physiological artifacts in *f*NIRS is an important consideration with regard to reaping the full potential of the technique for real-life applications (Jahani et al., 2018). In the present study, we applied tracking methods to identify sources of noisy data. The synchronisation of the different

Figure 12

Diagrammatic Representation of the Sources, Detectors, and Channel Layout



Note. Adjacent sources and detectors were 3 cm apart.

systems was controlled by means of Matlab algorithms. The central command computer controlled for motor tasks; it sent markers to the other apparatus – including the *f*NIRS system – to segment the times of onsets and offsets in an automated manner. A similar marking system was used in our previous studies (e.g., Blampain et al., 2018), which revealed a synchronisation error of ~35 ms. Visual tags were used to identify the beginning and end of each trial, with specific tags for each trial type.

CARDIORESPIRATORY MONITORING. By use of the Fourier transform method, both heart and respiratory rates can be identified in the *f*NIRS frequency spectrum. The ability to identify these two frequency components serves to ensure the validity of *f*NIRS measures. In terms of frequency, the neurophysiological detail in the *f*NIRS signals is lower than that of both heart and respiratory rates (~2 Hz and ~0.3 Hz, respectively; Pinti et al., 2019). Thus, these physiological components were filtered out, which restricted any potential contamination from the raw *f*NIRS signal.

Cardiorespiratory monitoring was done using the MP150 Biopac system (Biopac Systems, Goleta, CA), complemented with two dedicated add-on wearable devices. To avoid recording movement artefacts, heart rate (HR) data (Hz) were captured by use of an ECG Bionomadix module (wireless transmitter and RPEC-R amplifier) and low-pass filtered to 1 Hz. Two disposable patch electrodes were placed on the partic-

ipant's right and left clavicles. Respiration rate (Hz) was recorded using the TSD201 respiratory effort transducer, which was wired to the RSP100C amplifier. This respiratory belt was placed around the chest wall, at the level of the sternum. Sampling frequency was set to 250 Hz. Data acquisition was facilitated by the Acq*Knowledge* software that is included in the MP system.

HEADSET POSITION TRACKER. Data were collected using three Oqus 5+ cameras (Qualisys MoCap, Göteborg, Sweden) to control for any shift in the headset. The spatial positions were measured in real time using three spherical passive markers taped to the participant's right temple and headset (with the use of one and two markers, respectively). The distance between the temple marker and each of the two headset markers was computed (in cm) based on Cartesian coordinates (i.e., x, y, and z). The spatial accuracy of the system is 0.5 mm for each dimension of 3D space.

To verify the occurrence of a *f*NIRS helmet shift, a deformation calculation of the area of the planar triangle connecting the 3D markers was used. This was referred to as the *mesh area*. Notably, if the 3D markers remain in the same place with respect to each other, the mesh area remains constant. On the other hand, if the two markers of the headset move relative to the reference marker (i.e., temple marker), the mesh area is modified.

The mesh area between the three markers was computed using a scalar product (Equation 1). If $\overrightarrow{M_0M_1} \cdot \overrightarrow{M_0M_2}$ remained constant over time with an acceptable error threshold, an absence of deformation of the mesh was considered and indicative of an absence of headset shift. In the present study, the error threshold ϵ was set to 10 mm, which corresponds to the degree of spatial resolution of the *f*NIRS optical imaging technique (Quaresima & Ferrari, 2016). The variation Δ_{mesh} of the $\overrightarrow{M_0M_1} \cdot \overrightarrow{M_0M_2}$ value was computed. If this value exceeded 15%, which corresponds with ϵ, the participant's data from that block of trials as well as from subsequent blocks were removed for the purposes of statistical analysis, as it was difficult to determine the exact sources of the recorded hemodynamic signals.

4.2.4 *Statistical Analyses*

4.2.4.1 *Data Eligible for Analysis*

HbT reflects the overall changes in corpuscular blood volume of the sampling volume. Because HbT is a summation of HbO_2 and HHb changes (see Equation 7), it was not statistically analysed. The behavioural data were analysed and reported in a supplementary online file. HHb and HbO_2 data were analysed only from those blocks of trials characterised by (a) at least 70% level of behavioural accuracy, and (b) an absence of headset shift. A participant's entire data set was removed if > 25% of his data were ineligible and any excluded participants were replaced.

Given that an absence of cerebral activation can be informative, both activated and non-activated channels were taken into consideration. In addition, the ratio of activated to non-activated channels (i.e., if $B_{X,i}$ and $P_{X,i}$ are significantly different) was reported for each trial. Only HbO_2 data were used to support or refute hypotheses. However, HHb data were also statistically analysed to improve specificity of *f*NIRS

signals, as recommended in the *f*NIRS literature (e.g., Leff et al., 2011; Tachtsidis & Scholkmann, 2016). The alpha level was set at $p < .05$ for all statistical analyses.

4.2.4.2 *Analyses Undertaken*

CLASSIC NULL-HYPOTHESIS SIGNIFICANCE TESTS. The dependent variables, $\bar{\Delta}_{HbO_2}$ and $\bar{\Delta}_{HHb}$ for each of the two regions of interest were analysed. To examine H_1 and H_2, a oneway RM ANOVA (Externally-Paced Tempo [300, 500, 1200 ms]) was applied. Normality was checked using the Shapiro–Wilk test; if violated, the data were normalised using a transformation that was contingent on data distribution curves (e.g., log10). Where Mauchly's tests indicated violations of the sphericity assumption, Greenhouse–Geisser corrections were applied. Tukey post hoc tests were used where necessary (see Table 3).

EQUIVALENCE TESTS. It is not acceptable to use nonsignificance of the interaction term from an analysis of variance (ANOVA) to claim the absence of an interaction effect (Cribbie et al., 2016). Consequently, to confirm that similar effects of externally-paced tempo were observed regardless of the task complexity (H_3), TOSTs were used (Lakens et al., 2018). In this procedure – referred to as *equivalence testing* – the SESOI is used to test whether an effect is sufficiently close to zero to reject the presence of a meaningful difference (Harms & Lakens, 2018, p. 385). The results of both t tests needed to reach significance in order for equivalence to be claimed. To date, the TOST procedure has only been used in a oneway ANOVA design (Campbell & Lakens, 2020), and has yet to be extended to interaction effects. Accordingly, TOST were computed on the *change score* (i.e., difference between the 300- and 1200-ms tempo trials) between (a) the simple and moderate tasks, (b) the simple and complex tasks, and (c) the moderate and complex tasks. TOSTs were computed using the TOSTER R package for paired-samples t tests (Lakens, 2017).

4.2.4.3 *Outcome-neutral validation tests*

The *f*NIRS technique is rather new in the field of human brain sciences and so defining a positive control provides many challenges. Consequently, a negative control condition was included by placing an additional channel over the occipital brain region (Broadmann's area 18). This region is involved primarily in visual perception and so its activation should remain fairly consistent across pacing conditions and motor tasks. Accordingly, TOSTs (Lakens et al., 2018) were computed for paired-samples t tests between the baseline $B_{X,occipital}$ and the plateau $P_{X,occipital}$ for each block of trials. Statistically nonsignificant differences provided a means by which to confirm that observed prefrontal and motor activations are related to the modulation of motor tempo. If differences were detected over the occipital brain region, the delta activation was removed from all other delta values.

4.3 RESULTS

4.3.1 *Behavioural Data*

4.3.1.1 *Time-Interval Accuracy*

The RM ANOVA showed a significant main effect of motor tempo, $F(2, 24) = 6.88$, $p = .004$, $\eta_p^2 = .36$, with more IRI_{error} in the 300 ms ISI ($M = 10.79$, $SD = 3.39$) than in the 500 ($M = 8.54$, $SD = 2.84$) and 1200 ms ISI conditions ($M = 8.23$, $SD = 2.74$; Figure 13). The main effect of task complexity was also significant, $F(2, 24) = 77.86$, $p < .001$, $\eta_p^2 = .87$, with a smaller IRI_{error} in the simple ($M = 4.51$, $SD = 1.62$) and moderate tasks ($M = 5.89$, $SD = 1.59$) compared to the complex task ($M = 17.17$, $SD = 5.75$). The Motor Tempo $\times$ Task Complexity interaction was nonsignificant ($p = 0.117$). Overall, the results indicated that participants made more timing errors under a fast externally-paced tempo and when the task was complex.

4.3.1.2 *Spatial Accuracy*

The RM ANOVA showed a significant main effect of motor tempo, $F(2, 24) = 20.38$, $p < .001$, $\eta_p^2 = .63$, with the spatial errors decreasing from the 300 ($M = 42.75$, $SD = 13.04$) to the 1200 ms ISI ($M = 24.58$, $SD = 11.86$). The main effect of task complexity was also significant, $F(2, 24) = 78.88$, $p < .001$, $\eta_p^2 = .87$, with fewer spatial errors in the simple task ($M = 9.56$, $SD = 2.61$) than in the complex one ($M = 22.34$, $SD = 14.98$), and in the complex than in the moderate task ($M = 100.73$, $SD = 16.53$). The Motor Tempo $\times$ Task Complexity interaction was significant, $F(4, 48) = 8.54$, $p = .001$, $\eta_p^2 = .42$. This indicated that spatial errors were smaller in the simple task than in the complex one in the 300 ($p < .001$) and the 500 ms ISI conditions ($p < .001$); however, the spatial errors were similar in the simple and complex tasks in the 1200 ms ISI condition (Figure 13). Overall, the results showed that participants made more spatial errors when required to move through space quickly.

4.3.2 *Headset Position Tracker*

The absolute variation Δ_{mesh} did not exceed the 15% threshold for any of our participants ($M = 0.91$, $SD = 0.87$). The maximum percentage change observed was 3.13%. Overall, the data confirmed the absence of an *f*NIRS helmet shift, meaning that the 3D markers held the same relative positions throughout the experimental trials.

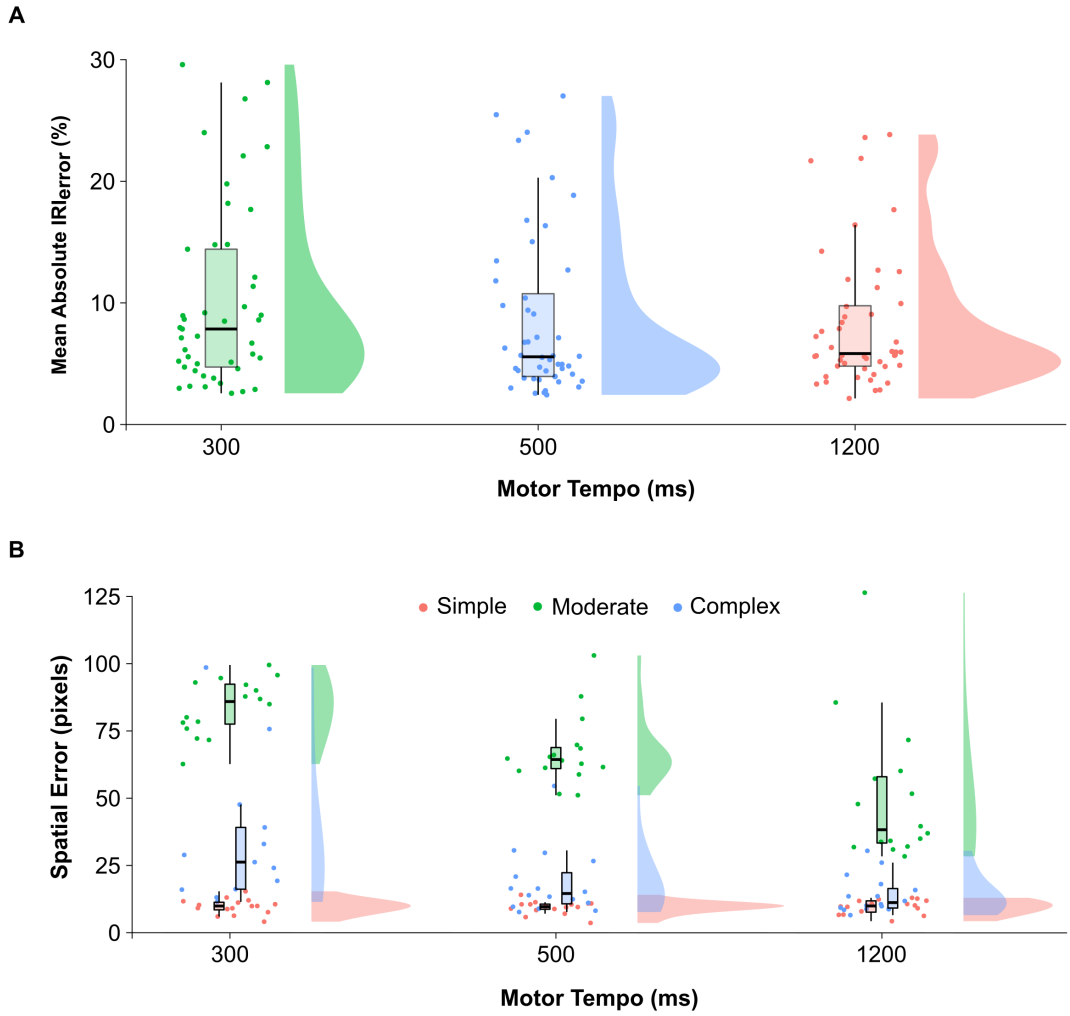
4.3.3 *fNIRS Data*

4.3.3.1 *Preprocessing*

Given that our *f*NIRS system does not provide access to raw intensities, preprocessing was performed directly on Δ_{HbO_2} and Δ_{HHb} concentrations. This was achieved using Matlab, with both personal code and algorithm adapted from the Matlab-based toolbox Homer2 (Massachusetts General Hospital, Boston, MA, USA). The preprocessing steps are detailed in Figure 14.

Figure 13

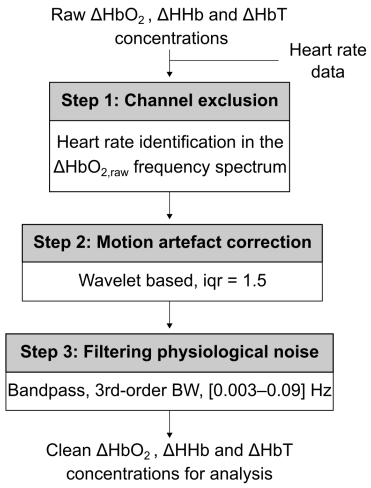
Behavioural Results for Each Experimental Condition



Note. Panel A: Mean IRI_{error}. Box plots and density distributions are displayed for each designated motor tempo. Each dot represents an individual participant. IRI = inter-response interval. Panel B: Mean spatial errors. Box plots and density distributions are displayed for each designated motor tempo and level of task complexity. Each dot represents an individual participant.

The *f*NIRS literature details several filtering methods (Herold et al., 2018; Hocke et al., 2018; Pinti et al., 2019) and a hybrid filtering of the *f*NIRS time-series was applied in the present study (see Jahani et al., 2018). First, the wavelet-based method was used to perform motion-artefact correction, as it appeared to apply particularly well to our dataset, and has been shown to be relatively efficient (Hocke et al., 2018). Second, *f*NIRS data were bandpass filtered to remove physiological noise that was concomitant to the task-induced hemodynamic activity.

Figure 14
Preprocessing Pipeline of fNIRS Data



Note. HbO_2 = oxygenated haemoglobin; HHb = deoxygenated haemoglobin; iqr = interquartile range; BW = Butterworth filter.

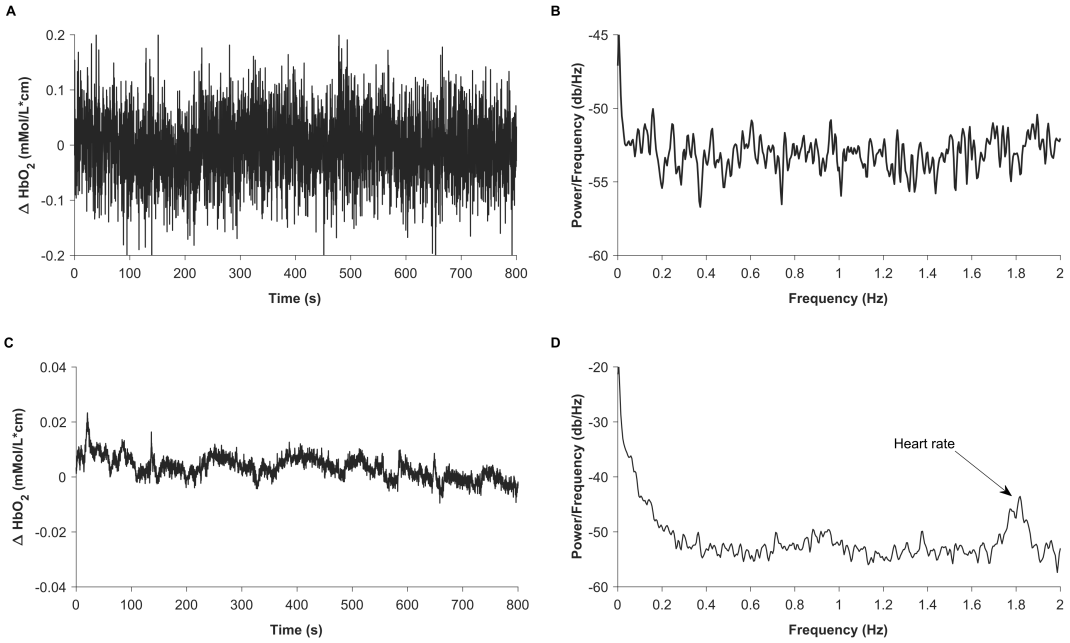
CHANNEL EXCLUSION CRITERION. The first mandatory step was to control for the optical-coupling quality of the acquired *f*NIRS data (Orihuela-Espina et al., 2010; Pinti et al., 2019; Scholkmann et al., 2017). Optical coupling is characterised by the presence of heart-beat oscillations within the *f*NIRS signals. A frequency inspection of the raw *f*NIRS time series enabled the exclusion of channels with a poor optical coupling (i.e., an absence of HR in the power spectrum of *f*NIRS signals). Only Δ_{HbO_2} raw data were analysed, as HbO_2 is more sensitive to cardiac oscillation than HHb (Pinti et al., 2019). A two-step process was used to check the 45 channels for each participant: First, applying PSD (i.e., frequency domain) to the raw data, the frequency corresponding to maximal peak in the 50–160 beat-per-minute (bpm) range was detected. Second, to guarantee that the identified frequency was indeed the HR frequency, it was compared to the HR measurements provided by the Biopac system, with a tolerance threshold of 7 bpm.

Following the aforementioned steps, three participants were excluded due to an absence of heart beat oscillations in the *f*NIRS signal across all channels pertaining to at least one region of interest. In addition, the channels for which we failed to identify cardiac-frequency component for all participants were excluded from subsequent statistical analyses. Overall, 34.8% of channels were rejected on this basis. Examples of both acceptable and excluded channels are shown in Figure 15.

MOTION CORRECTION: WAVELET FILTERING. *f*NIRS signals recorded during body movements are prone to motion artefacts. Accordingly, motion correction was performed to remove motion-induced sharp and fast skips from the raw *f*NIRS time series (see Figure 16). To this end, the wavelet-based smoothing method described by Molavi and Dumont (2012) and implemented in Homer2 (hmrMotionCorrect_Wavelet function, interquartile-range [iqr] = 1.5) was adapted to process con-

Figure 15

Raw Data and Power-Spectrum Density of Two Levels of Signal-to-Noise Ratio



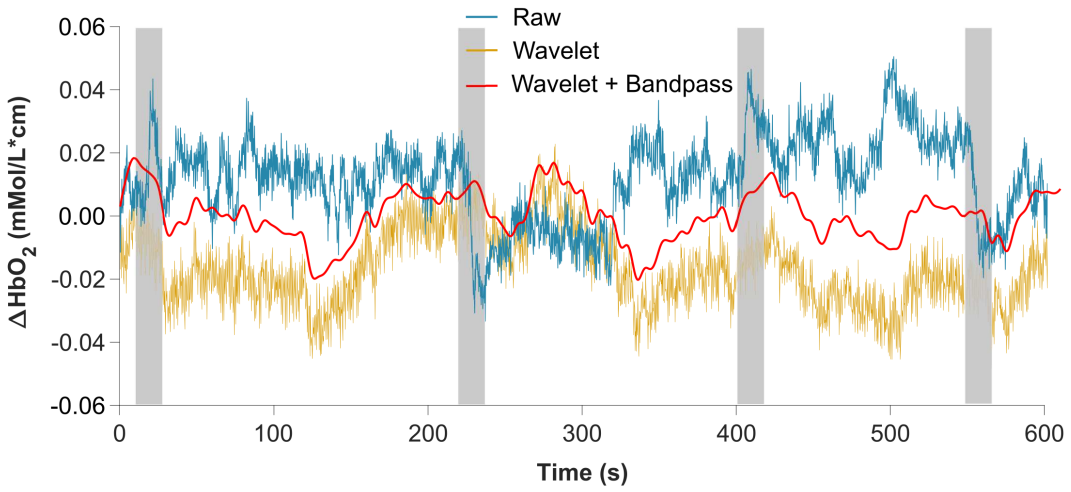
Note. Samples of Δ_{HbO_2} recorded on channel 17 for two participants (left), and their respective power spectrum (right). Heart rate frequency was not identified in the power-spectrum density for a time-series with a poor signal-to-noise ratio (SNR; top right), but present with high SNR (bottom right).

centrations rather than of optical densities. The motion-corrected data were visually inspected to ensure that the selected iqr value was well suited to the present dataset.

BANDPASS FILTERING OF PHYSIOLOGICAL NOISE. Haemodynamic responses elicited by a cognitive process are jeopardised by physiological processes that are not directly linked to the task being undertaken (Scholkmann et al., 2014; Tachtsidis et al., 2004). To minimise the effects of spontaneous hemodynamic activity – HR (~1 Hz), breathing rate (~0.3 Hz), Mayer waves (i.e., arterial pressure oscillations; ~0.1 Hz), and very low frequency oscillations (VLF, < 0.04 Hz) – motion-corrected *f*NIRS signals were bandpass filtered.

A third-order Butterworth filter was applied to extract relevant frequencies (see Figure 16). The highpass was set at 0.003 Hz to reject both cardiac and breathing rates and parts of Mayer oscillations. The lowpass was set to 0.09 Hz to preserve the stimulation protocol frequency (1 / (task + rest) = 0.01 Hz) without attenuation (0 dB flat frequency band of the filter). The 2nd and 3rd harmonics that contained important information were also preserved (Pinti et al., 2019). Figure 16 summarises the steps taken in the hybrid filtering process.

Figure 16
Filtering of the fNIRS Signal



Note. Example of the filtering of motion artefact (wavelet based, brown) and physiological noise (bandpass, red) from Δ_{HbO_2} data (channel 33, blue). Areas highlighted in gray represent motion-kind and baseline shift artefacts.

4.3.3.2 *Outcome-Neutral Validation Tests*

The TOST procedure (SESOI = 0.8) showed that both t tests were significant, $t_{upper}(15)$ = -4.48, $p < .001$, $t_{lower}(15)$ = 1.92, $p = .037$. Thus, equivalence was established, confirming that occipital activations remained similar across tempo conditions and levels of task complexity.

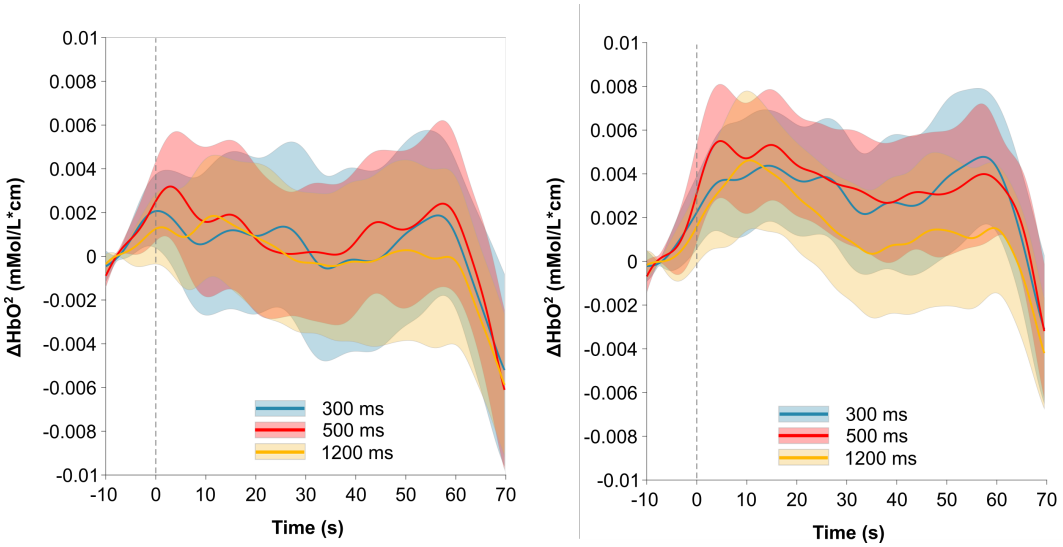
4.3.3.3 *Oxygenated Hemoglobin*

To detect non-activated channels, $\bar{\Delta}_{HbO_2}$ was tested against zero by means of a one-sided t test within each of the 45 channels. To account for multiple comparisons, Bonferroni corrections were applied (.05 ÷ 45; $\alpha = .001$). Results showed that all $\bar{\Delta}_{HbO_2}$ were significantly different from zero. Collectively, the results indicate that 100% of the channels were activated.

MOTOR CHANNELS. The RM ANOVA showed a significant main effect of motor tempo, $F(2, 30) = 5.77$, $p = .007$, $\eta_p^2 = .28$, with a smaller $\bar{\Delta}_{HbO_2}$ in the 1200 ms ISI (M = 1.85, SD = 6.52) than in the 300 (M = 4.94, SD = 7.60, d_z = 0.43) and the 500 ms ISI conditions (M = 4.23, SD = 7.26, d_z = 0.34; Figure 17). Note that the effect size of both contrasts was larger than the required SESOI (see Table 3), which indicated that the effects were sufficiently strong to be considered meaningful.

The TOST procedure computed on the change score between the simple and moderate tasks showed that both t tests were significant, $t_{upper}(15)$ = -2.97, $p = .005$, $t_{lower}(15)$ = 1.97, $p = .034$. However, neither of the TOST procedures computed on

Figure 17
fNIRS Data for Each Experimental Condition



Note. Panel A: Mean $\bar{\Delta}_{HbO_2}$ for each motor tempo in the prefrontal channels. The 95% confidence intervals are represented by the shaded area that surrounds each trace. Panel B: Mean $\bar{\Delta}_{HbO_2}$ for each motor tempo in the motor channels. The 95% confidence intervals are represented by the shaded area that surrounds each trace.

the change score between (a) the simple and complex tasks (p_{upper} = .003, p_{lower} = .159), and (b) the moderate and complex tasks (p_{upper} = .002, p_{lower} = .183) reached significance. Overall, the results confirmed similar effects of motor tempo across the simple and moderate tasks over the motor areas (see Table 4).

PREFRONTAL CHANNELS. The RM ANOVA showed a significant main effect of motor tempo, $F(2, 30) = 3.93$, p = .030, η_p^2 = .21, with a larger $\bar{\Delta}_{HbO_2}$ in the 500 ms ISI (M = 3.75, SD = 6.51) than in the 1200 ms ISI condition (M = 1.06, SD = 5.52, d_z = 0.44; Figure 17). Note that the effect size of the contrast was larger than the required SESOI, which indicated that the effect was sufficiently strong to be considered meaningful.

The TOST procedure computed on the change score between the simple and moderate tasks showed that both t tests were significant, $t_{upper}(15)$ = -2.56, p = .011, $t_{lower}(15)$ = 2.38, p = .015. However, neither of the TOST procedures computed on the change score between (a) the simple and complex tasks (p_{upper} = .007, p_{lower} = .072), and (b) the moderate and complex tasks (p_{upper} = .007, p_{lower} = .069) were significant. Overall, these results indicated similar effects of motor tempo across the simple and moderate complexity tasks over the prefrontal areas (see Table 4).

4.3.3.4 *Deoxygenated Haemoglobin*

MOTOR CHANNELS. The RM ANOVA ran on the $\bar{\Delta}_{HHb}$ was nonsignificant (p = .749). The TOST procedure computed on the change score between the simple and moderate tasks showed that both t tests were significant, $t_{upper}(15)$ = -2.20, p = .022, $t_{lower}(15)$ = 2.75, p = .008. However, neither of the TOST procedures computed on the

Table 4
Oxyhaemoglobin and Deoxyhaemoglobin Change Scores Over the Motor and Prefrontal Regions of Interest

Regions of Interest	Oxyhaemoglobin		Deoxyhaemoglobin	
	M	*SD*	*M*	*SD*
Motor				
Simple	0.97	8.28	-0.15	1.99
Moderate	2.22	9.33	-0.36	2.15
Complex	5.54	7.65	0.46	3.09
Prefrontal				
Simple	0.51	6.61	-0.29	2.81
Moderate	0.75	8.06	0.04	1.50
Complex	2.45	8.24	0.40	3.45

Note. Means and standard deviations for oxyhaemoglobin and deoxyhaemoglobin change scores (i.e., $\bar{\Delta}_{HbO_2}$ 300 ms - $\bar{\Delta}_{HbO_2}$ 1200 ms) for each motor task. A positive value indicates higher activations for 300 vs. 1200 ms.

change score between (a) the simple and complex tasks (p_{upper} = .008, p_{lower} = .062), and (b) the moderate and complex tasks (p_{upper} = .007, p_{lower} = .073) were significant. Overall, these results indicated similar effects of motor tempo across the simple and moderate complexity tasks over the motor areas (see Table 4).

PREFRONTAL CHANNELS. The RM ANOVA performed on the $\bar{\Delta}_{HHb}$ was non-significant (p = .529). The TOST procedure computed on the change score between the simple and moderate tasks showed that both t tests were significant, $t_{upper}(15)$ = -2.92, p = .005, $t_{lower}(15)$ = 2.03, p = .030. The TOST procedure computed on the change score between the moderate and complex tasks showed that both t tests were significant, $t_{upper}(15)$ = -2.63, p = .011, $t_{lower}(15)$ = 1.82, p = .047. However, the TOST procedure computed for the change score between the simple and complex tasks was nonsignificant (p_{upper} = .007, p_{lower} = .071). Overall, these results indicated similar effects of motor tempo over the prefrontal area across the simple and moderate complexity tasks, and in the moderate and complex tasks (see Table 4).

4.3.4 *Exploratory Analyses*

Through visual inspection, we noticed that HbO_2 began to increase just prior to initiation of the task (see Figure 17). It is notable that the epoch used to compute $B_{HbO_2,i}$ (i.e., from 5 s to 10 s before the trial onset) coincided with when HbO_2 had already started to increase. To make $B_{HbO_2,i}$ more representative of the baseline level, additional analyses were applied for which $B_{HbO_2,i}$ was taken from 20 s to 10 s prior to trial onset. These findings are presented in the paragraphs that follow.

The RM ANOVA performed on the motor channels showed a significant main effect of motor tempo, $F(2, 30) = 7.04$, $p = .003$, $\eta_p^2 = .32$, with a smaller $\bar{\Delta}_{HbO_2}$ in the 1200 ($M = 3.06$, $SD = 5.21$) than in the 300 ms ISI ($M = 6.74$, $SD = 6.65$, $d_z = 0.59$) and the 500 ms ISI conditions ($M = 5.94$, $SD = 6.05$, $d_z = 0.50$). Note that the effect size of both contrasts was larger than the required SESOI, which indicated that the effects were strong enough to be considered meaningful. None of the TOST procedures computed on the change score between (a) the simple and moderate tasks ($p_{upper} = .001$, $p_{lower} = .093$), (b) the simple and complex tasks ($p_{upper} = .005$, $p_{lower} = .097$), and (c) the moderate and complex tasks ($p_{upper} = .009$, $p_{lower} = .056$) were significant. Overall, these results indicate dissimilar effects of motor tempo over the motor region. A oneway RM ANOVA (Task Complexity [simple, moderate, complex]) was also computed but found to be nonsignificant ($p = .966$).

The RM ANOVA performed on the prefrontal channels showed a significant main effect of motor tempo, $F(2, 30) = 6.11$, $p = .006$, $\eta_p^2 = .29$, with a larger $\bar{\Delta}_{HbO_2}$ in the 500 ($M = 5.81$, $SD = 5.23$) than in the 1200 ms ISI condition ($M = 2.83$, $SD = 5.14$, $d_z = 0.57$). Note that the effect size of the contrast was larger than the required SESOI, which indicated that the effect was sufficiently strong to be considered meaningful. The TOST procedure computed on the change score between the simple and moderate tasks showed that both t tests were significant, $t_{upper}(15) = -2.97$, $p = .005$, $t_{lower}(15) = 1.97$, $p = .034$. The same effects were observed between the simple and complex tasks, $t_{upper}(15) = -2.64$, $p = .011$, $t_{lower}(15) = 1.82$, $p = .047$, and between the moderate and complex tasks, $t_{upper}(15) = -2.38$, $p = .017$, $t_{lower}(15) = 2.08$, $p = .030$. Overall, these results confirmed similar effects of motor tempo over the prefrontal region, regardless of level of task complexity.

4.4 DISCUSSION

The main purpose of the present study was to investigate frontal brain activity under conditions of different speeds of motor execution. Three forms of upper-limb movement were used as SMS tasks and performed at fast (i.e., 300 ms), natural (i.e., 500 ms), and slow paces (i.e., 1200 ms). H_1 was not supported as performing the tasks at spontaneous motor tempo did not yield less prefrontal and motor activation than moving faster or slower. Action production at fast tempi led to greater motor oxygenation compared to action production at slow tempi, which replicated the previously-reported effect of larger increases in HbO_2 over the motor cortex when a movement is executed at a fast pace (Kuboyama et al., 2004, 2005). However, moving at slow tempi did not lead to greater increases in cerebral oxygenation over the prefrontal lobe when compared to the faster tempo. Accordingly, H_2 is partially verified. Equivalence tests on task complexity were significant for the two finger-tapping tasks only, and not for the continuous-drawing task. Hence, H_3 was also only partially verified.

4.4.1 *Cerebral Responses*

Collectively, the present findings demonstrated the ability of *f*NIRS to dissociate the involvement of different cognitive mechanisms as a function of task constraints. The

first important result is that the motor areas were activated to a greater degree when producing actions at fast vs. slow tempi. In addition, TOST tests and descriptive data confirmed that this pattern of results was potentiated in the complex task (i.e., circle drawing; see Table 4). These findings are congruent with the *dynamic systems* approach of motor timing, in which behaviour is described as "the emergent product of a self-organising, multicomponent system evolving over time" (Perone & Simmering, 2017, p. 44). Indeed, behavioural studies have reported that the production of fast movements is dependent on dynamic processes (Huys et al., 2008). In this respect, the temporal organisation of movements performed at 300 ms of ISI would emerge from the regularities of body-dynamics (e.g., mass, length, velocity; Zelaznik et al., 2002). Hence, there would be less cognitive control applied upon motor execution (Lemoine, 2007). The findings of the present study extend the behavioural literature by providing evidence that fast movement production is underpinned predominantly by central and non-reflective motor processes.

The second important result is that performing a task at a slow pace did not induce larger prefrontal hemodynamic responses when compared to performing at a fast pace. Explanation for this unexpected finding lies with a measurement issue. Being limited to 47 channels by our *f*NIRS system, we were not able to optimally cover the prefrontal areas of the brain: A unique row of channels is accounted for on the dorsolateral cortex. Therefore, it is possible that the ability to modulate motor tempo according to environmental constraints is underpinned by cognitive functions that might be pinpointed further forward in the brain.

By way of illustration, the medial prefrontal cortex has been proposed to control the adaptive responses to context, location, and events (Di Pellegrino et al., 2007; Euston et al., 2012), and could play a central role in performing a motor task at a slow tempo. However, it would not have been recorded with the current *f*NIRS measurement configuration. Even further frontal is the orbitofrontal cortex, which is implicated in response inhibition (Evans et al., 2004; Horn et al., 2003). In futures studies, there will be a clear need for more accurate contrasts of the activation loci evident across different prefrontal areas. This will facilitate delineation of the frontal-cognitive processes that underlie the ability to execute slow movements.

4.4.2 *Spontaneous Motor Tempo*

It is notable that motor timing at the spontaneous motor tempo led to greater prefrontal activation. It could be that the recorded activation does not originate from the dorsolateral cortex but from the supplementary motor area (SMA), which is located close to the recorded channels. Using the fOLD toolbox (*f*NIRS Optodes' Location Decider; Morais et al., 2018), we found that the recorded prefrontal activation had a ~25% likelihood of having originated from the SMA. Relative to other neuroimaging techniques (e.g., EEG), the *f*NIRS spatial resolution is quite good; nonetheless, the measured activity is localised within the brain with an error of ~1 cm (Herold et al., 2018). Therefore, the *f*NIRS technique may not afford sufficient fidelity to distinguish dorsolateral prefrontal cortex activity from SMA activity.

Macar et al. (2006) proposed that, as part of the striato-cortical pathway, the SMA plays a key role in time processing. In previous studies with *f*MRI, the pre-SMA

was found to be more activated when participants were directed to selectively attend to time in perceptual-timing tasks (Coull, 2004; Coull et al., 2004). It is noteworthy that the SMA was more involved for tempi close to spontaneous pace (i.e., 540 ms ISI) than for slower tempi (i.e., 1080 ms ISI; Coull et al., 2012). There is similarity with the present findings, which show significantly greater prefrontal activation in spontaneous vs. slow-pace movement using analogous time intervals. In addition, patients with SMA lesions have been reported to be impaired in rhythm-reproduction tasks in the absence of auditory cues; nonetheless, they were perfectly able to produce rhythms when auditory pacing was provided (Halsband et al., 1993). Accordingly, the SMA may be more strenuously involved in internally-generated movements rather than in the external guidance of timed movements (Rao et al., 1997).

The increase of prefrontal activation identified in the present study was occasioned by motor execution at a spontaneous pace (i.e., the instinctive speed associated with self-initiated action). As scientific knowledge stands, the cerebral correlates of motor production at a spontaneous motor tempo are unclear. A plausible hypothesis emanating from the present findings is that the SMA, and more specifically the pre-SMA, which has projections to and from the prefrontal cortex (Kim et al., 2010), serves a pivotal role in motor timing at (close-to-) spontaneous pace.

4.4.3 *Behavioural Outcome*

An original contribution of the present study concerns the three forms of upper-limb movement that were used to control for motor complexity. The behavioural results indicated that participants were less accurate in their time-interval production when they performed the complex (i.e., circle-drawing task) vs. the easier tasks (i.e., finger-tapping and pointing tasks). The same pattern of results was found using *f*NIRS: Identical effects of externally-paced tempo were observed for both the prefrontal and motor areas between the simple and moderate tasks, but not between these tasks and their complex counterpart. Accordingly, it seems that the performance of a timing task is more laborious in continuous motion than in discrete actions.

Discrete actions are characterised by a recognisable beginning and end; thus, they are much easier to synchronise with external events than continuous movements, for which there is no recognisable beginning and end. In the present study, motor activation could have been more salient when motor-timing control was challenging. Interestingly, the complementary analysis (performed on the first peak of hemodynamic activation) showed that an externally-paced tempo elicited similar effects regardless of motor complexity in the prefrontal cortex. Conversely, the three equivalence tests failed to reach significance in terms of the activation of motor areas. This finding suggests that the three upper-limb movements required different planning and execution strategies, but similar degrees of cognitive control for performance outcome.

4.4.4 *Strengths and Limitations*

The combination of *f*NIRS measurement with physiological indices has been advocated in recent years and referred to as SPA-*f*NIRS (Scholkmann et al., 2017). The

*f*NIRS technique enables the researcher to draw inferences about neural activity through the assessment of cerebral blood oxygenation. However, given that cardiac contractions contribute significantly to cerebral oxygen supply, the frequency of these contractions must be identified in the *f*NIRS signal of interest. Without such identification, the recorded signal might only contains non-physiological fluctuations. In the present study, the validity of the recorded *f*NIRS signal was verified through detailed observation of the relevant physiological information derived from the *f*NIRS channels (i.e., HR and respiratory frequency; see Figure 15). Collectively, the preprocessing data confirmed that the application of *f*NIRS to motor paradigms is a scientifically legitimate endeavour. Furthermore, we illustrated the importance of using physiological measurements to identify and select the channels of interest. Therefore, it is evident that SPA-*f*NIRS should be used in a systematic manner to verify that *f*NIRS data are sound, even in experimental paradigms that do not involve movement-based tasks.

The methodological advancement evident in the present study entails a rigorous procedure for the acquisition and processing of *f*NIRS data in the realm of whole-body movement. First, a 3D reconstruction of the headset position on the participant's head was used. This control is of paramount importance, as it enables the researcher to ascertain the precise location of the recorded *f*NIRS signal throughout an experimental session. In the current study, no *f*NIRS headset shifts were detected (on average, < 1% of variation during the experimental session), even in tasks requiring moving through space (e.g., the circle-drawing trials). Second, channel selection was undertaken to ascertain whether cardiac frequency was visible in the *f*NIRS signals (Pinti et al., 2019). Through this preprocessing method, only those channels with meaningful inputs were kept in the regions of interest. Finally, a hybrid filter technique that was applied proved effective in removing instrumental noise, motion-related artefacts, and physiological oscillations (for a review of noise source in *f*NIRS signals, see Herold et al., 2018) without overfiltering the signal, which seems to be a common phenomenon in the NIRS literature.

In terms of limitations of the present study, the three types of upper-limb movements that were chosen are simple laboratory-based tasks that have limited ecological validity. In addition, it is possible that the natural-pace condition did not best reflect the spontaneous motor tempo of a few participants. A condition developed from prior measurement of each participant's spontaneous motor tempo could have enhanced internal validity somewhat. The decision to select only participants with very short hair (< 1 cm) is also acknowledged as a minor limitation. Given that only male participants were recruited, we cannot readily generalise the findings to both sexes.

4.4.5 *Future Directions*

The present work serves to illustrate the technical challenges related to using whole-brain *f*NIRS in movement paradigms. Nonetheless, a few recent articles providing recommendations for *f*NIRS application are beginning to emerge in the scientific literature (e.g., Herold et al., 2018; Perrey, 2014; Pinti et al., 2019). It is hoped that researchers will take up the gauntlet of investigating cognitive processes underlying

time production and use realistic, whole-body movements in so doing. Such explorations will represent a meaningful contribution to the knowledge base of cognitive neuroscience by providing a broader picture of how the brain modulates motor timing.

Future research might also address the role of the brain's functional connectivity in the adaptation of motor timing (see Vergotte et al., 2018, 2017). The assessment of *f*NIRS connectivity between the prefrontal cortex and motor areas holds potential to provide valuable insights on the cerebral dynamics underlying time production. This form of rich detail is obfuscated when researchers focus solely upon the activation pattern of one or two regions of interest.

From a methodological point of view, future research will need to tackle the dissociation of prefrontal from SMA activations. With this aim in mind, it will be appropriate to take anatomical specificity into account through tailoring the placement of *f*NIRS channels to the brain morphology of each participant; this *neuronavigational approach* will substantially increase the accurate identification of the brain areas of interest (Herold et al., 2018). Close attention will also need to be given to the choice of experimental motor tasks, as different brain patterns can be observed as a function of the discrete vs. continuous dimension of motor skill execution. Researchers might use naturalistic movements that mirror those used in everyday life, such as walking or cycling.

4.4.6 *Conclusions*

When examined collectively, the findings of Chapter 4 indicate that motor tasks performed either at a fast or slow tempo will result in differences in brain activation. *f*NIRS can be used to gain a fuller understanding of the brain dynamics involved in the modulation of motor tempo. Fast pacing relies on greater activity of the motor areas whereas moving at close-to-spontaneous pace places a heavier load on posterior prefrontal processes. These findings are consistent with the notion that two timing modes exist (see Huys et al., 2008; Madison & Delignieres, 2009); they confirm that the execution of fast movements (i.e., faster than the spontaneous motor tempo) depend on dynamic systems from which bodily movements emerge (Zelaznik et al., 2002). The effects of spontaneous motor pacing on prefrontal brain activity are possibly the result of the SMA involvement for motor execution at natural pace. With *f*NIRS technology, the scientific community has a means by which to unravel the mystery surrounding how the brain controls time production.

INTERMEDIATE SUMMARY

People are able to modify the spontaneous pace of their actions to interact with their environment and others. This ability is underpinned by high-level cognitive functions but little is known in regard to the brain areas that underlie such temporal control. A salient practical issue is that current neuroimaging techniques (e.g., EEG, *f*MRI) are extremely sensitive to movement, which renders challenging any investigation of brain activity in the realm of whole-body motor paradigms. Within the last decade, the noninvasive imaging method of *f*NIRS has become the reference tool for experimental motor paradigms due to its tolerance to motion artefacts.

The general aim of Chapter 4 was to examine the cerebral oxygenation of prefrontal and motor areas simultaneously during the execution of fast, close-to-SMT, and slow movements. A continuous-wave *f*NIRS system was used to record the prefrontal and motor haemodynamic responses of 16 participants, while they performed a spatial-tapping task varying in motor complexity and externally-paced tempi (i.e., 300, 500, 1200 ms). Results indicated that fast pacing relied on greater activity of the motor areas whereas moving at close-to-spontaneous pace placed a heavier load on posterior prefrontal processes.

Chapter 4 has been published in *NeuroImage* (2021). In addition, the results have been the subject of two conference presentations (2019, Brain Twitter Conference; 2nd Timing Research Forum, Querétaro, Mexico) and three poster presentations (2018, Biennial Meeting of the Society for *f*NIRS, Tokyo, Japan; 2020, Brain. Cognition. Emotion. Music. Conference, Canterbury, UK; 2021, Art in Motion, Munich, Germany).

Upper-limb tasks (e.g., finger tapping, circle drawing) are commonly used to investigate motor timing because they enable a high level of control in terms of motor output. Nonetheless, these artificial tasks are cognitively demanding and not representative of everyday-life motor behaviours. The general aim of Chapter 5 was to investigate the ecological validity of motor-timing tasks by providing a direct comparison among the tasks of finger tapping, foot tapping, and stepping on the spot.

5

FROM SIMPLE MOVEMENTS TO ECOLOGICAL MOTOR TASKS

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5.1 INTRODUCTION

The theoretical framework of embodied cognition asserts that there are reciprocal influences between body and brain (Wilson, 2002). In current theories of embodied-music cognition, the body is seen as a mediator for music perception (Leman et al., 2008). As commonly observed in everyday life behaviours, music can indeed generate the desire to move (e.g., tapping toe in time with a song). Sometimes, these natural musically-related behaviours are deliberately encouraged to serve a purpose, as when soldiers march to the beat of the drums, or train using drill songs. A further example is workers who often synchronise to music to facilitate the load of their physical movements when performing physical and repetitive tasks (McNeill, 1995).

The relationship between music perception and timed body movements is made possible through the predictability inherent in musical expectations. Over the last two decades, finger-tapping tasks have been extensively used in laboratory settings to portray a broad picture of the mechanisms underlying musically-synchronised behaviours (Chen et al., 2006; Drake et al., 2000; McPherson et al., 2018). Commonly described as SMS, tapping to the beat of a metronome involves the intentional temporal coupling of finger movements to a series of predictable events (i.e., beeps; Large, 2000). Performing an SMS task requires the cognitive ability to elaborate a representation of time-interval durations in order to predict when the next event will occur (i.e., predictive timing).

The synchronisation ability of an individual is measured as the difference (i.e., the asynchrony) between the targeted event and the motor action (Repp, 2005). Typically, healthy individuals tap approximately 30 ms too early, an anticipation error known as negative mean asynchrony (Aschersleben, 2002). Although the reasons for this phenomenon are not fully understood, the anticipation error is assumed to arise because the brain synchronises the sensory consequences of the action with the event (e.g., auditory tone) without counting for the afferent-conductance delay (Fleury et al., 1992).

To bypass these perceptual limitations, experimental paradigms often include a section during which the task is to be continued without the metronome. More specifically, the second section of the synchronisation–continuation task investigates the phenomenon described by Repp (2005) as "covert, internal synchronisation" (p. 969). In this instance, participants attempt to remain in synchrony with the memorised percept of the pacing cue provided during the synchronisation section, letting the

sequential action be entrained by an internalised representation of the metronome. In the continuation task, timing abilities are evaluated by measuring the mean and variance of the IRIs (Wilquin et al., 2018).

Motor timing is affected by the speed constraints set upon the task. Behavioural studies have suggested that predictions – which rely on the cognitive representation of the temporal intervals to reproduce – becomes too difficult when the tempi speed up (Guérin et al., 2021a). Rather than depending only on predictive timing processes, SMS to fast tempi emerge from oscillatory kinematic parameters (i.e., emergent timing; Dione & Delevoye-Turrell, 2015; Zelaznik et al., 2002). This oscillation frequency is directly influenced by the physical parameters of the agent, such as the mass and length of the limbs (Yu et al., 2003).

Experimental evidence showed that the best SMS performances in terms of both synchronisation (measured with the asynchrony) and timing accuracy (measured with the IRI) should occur within a synchronisation range of ISI of 400–700 ms, with a peak around 550 ms (Delevoye-Turrell et al., 2014). This pacing tempo corresponds to the SMT that has previously been reported in the general adult population (Repp & Su, 2013; Rose et al., 2020). The SMT has been referred to as a self-initiated pace observable in various rhythmical body movements (e.g., tapping, clapping, walking; MacDougall & Moore, 2005).

In lifespan studies of SMS abilities, a rise-and-fall pattern of motor-timing ability has been found, consistent with what is observed in other cognitive and motor functions (Drewing et al., 2006). Some researchers have suggested that SMS performances peak in middle-aged and decline from the early forties (Nagasaki et al., 1988; Salthouse, 1996), while other reported that SMS performances remained intact until at least the age of 75 years (Ivry & Keele, 1989). In the present study, the effects of ageing on motor timing in healthy adults were investigated using both asynchrony and IRI measurements in the classic synchronisation–continuation paradigm.

Metronome beeps are traditionally the stimulus used in rehabilitation programmes to improve motor-timing abilities (e.g., during gait; Dalla Bella et al., 2017; Wright et al., 2017) because they avoid the variety of emotional responses that can be engendered by music. Nonetheless, even if metronome beeps can assist in regulating movement patterns, they are boring, unpleasant, and less likely to enhance performance than musical cues (see Park et al., 2020). In sports science, music has been shown to be a performance-enhancing stimulus (Karageorghis et al., 2010). People can both synchronise with the musical meter and enjoy the extra-musical associations that music can evoke (Karageorghis, 2020). Music is indeed composed of several sonic features (e.g., melody, syncopation) that affect an individual's cognition and the subsequent production of motor behaviours (Karageorghis et al., 2012; Senn et al., 2019; Witek et al., 2014). In the present study, metronome beeps and musical excerpts were used to examine the effect of the pacing cue on SMS performances.

There is a methodological disconnect between (a) academic studies of motor timing that use finger-tapping paradigms and metronomes (see e.g., Repp, 2005; Wing & Kristofferson, 1973b) and (b) applied studies that focus on real-life behaviours (Repp & Su, 2013; Rodger & Craig, 2016). Finger tapping (i.e., movement of a simple effector) is the most common paradigm used to investigate motor timing because it enables an experimental focus purely on synchronisation abilities, without the need

to consider motor complexity (Drewing et al., 2006). Nonetheless, the embodied cognition framework questions the relevance of considering that similar findings are expected with or without the involvement of the body (Wilson, 2002). Body movements require much more than the simple flexion–extension of a finger. The intention to act involves motor preparation, with an additional consideration for the effort to move and perform (Blampain, 2019). Hence, testing motor timing performance in one movement modality may not necessarily transfer to SMS abilities in another (Repp, 2005; Rose et al., 2019).

The aim of the present study was to use the classic synchronisation–continuation paradigm to examine timing performance during the execution of motor behaviours varying in ecological validity. Three types of motor behaviours were used: finger tapping, foot tapping, and stepping on the spot. To investigate the effect of pacing cues in the production of synchronised and entrained motor behaviours, both metronomes beeps and musical stimuli were used. These auditory stimuli were presented at slow, medium, and fast paces – with the medium-tempo designation relating directly to SMT (McAuley et al., 2006; Rose et al., 2020; Van Noorden & Moelants, 1999). To assess possible age-related changes in motor timing abilities (Ivry & Keele, 1989; McAuley et al., 2006), the timing performances of both young and old adults were investigated.

It was hypothesised that: action production at slow and fast tempi would lead to more timing errors when compared to task execution at medium tempo (H_1); because of the complexity to control whole-body posture, in the synchronisation task, finger- and foot-tapping tasks would lead to fewer timing errors and variability than the stepping-on-the-spot task (H_2); in the continuation task, musical stimuli would lead to fewer timing errors and less variability when compared to metronome beeps (H_3); older adults would make more timing errors across the various SMS tasks when compared to their younger counterparts (H_4).

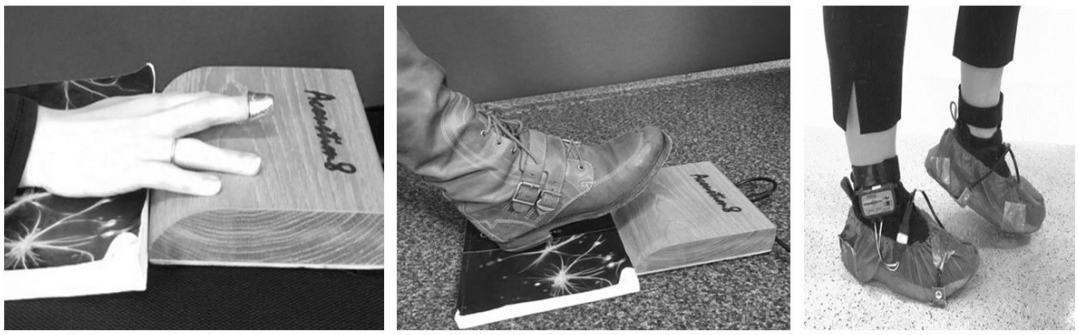
5.2 METHODS

5.2.1 *Participants*

Thirty-six right-handed/footed, healthy participants were recruited for the present study (21 women, 15 men; age range: 18–78 years; M_{age} = 45.3 years, SD = 26.8). The sample was split into two age groups of 18 participants each: a young-adult group (12 women, 6 men; age range: 18-20 years; M_{age} = 19.2 years, SD = 0.6) and old-adult group (8 women, 10 men; age range: 63-78 years; M_{age} = 71.5 years, SD = 4.9).

Participants were excluded from the study if they reported hearing loss or any musculoskeletal or neurological issues that significantly affected their walking. No participants were excluded on this basis. In addition, the Mini Mental State Examination (Folstein et al., 1975) was used to screen for cognitive deficits associated with dementia. The exclusion criteria were scores < 24. No participants were excluded on this basis. The study protocol was carried out in accordance with the principles enshrined in the Declaration of Helsinki. Participants gave written informed consent and ethical approval was granted by the ethics board of the University of Hertfordshire (see Appendix A).

Figure 18
Illustrations of the Experimental Setup and Apparatus for the Three Tasks



Note. Finger tapping (left), foot tapping (middle), and stepping on the spot (right).

5.2.2 *General Procedure and Experimental Design*

On arrival at the laboratory, the participant was fitted with transducers placed under their feet. Disposable shoe covers were used to protect the participant's shoes prior to the attachment of the transducers (see Figure 18, right panel). The heel strike apparatus was worn throughout the experimental session.

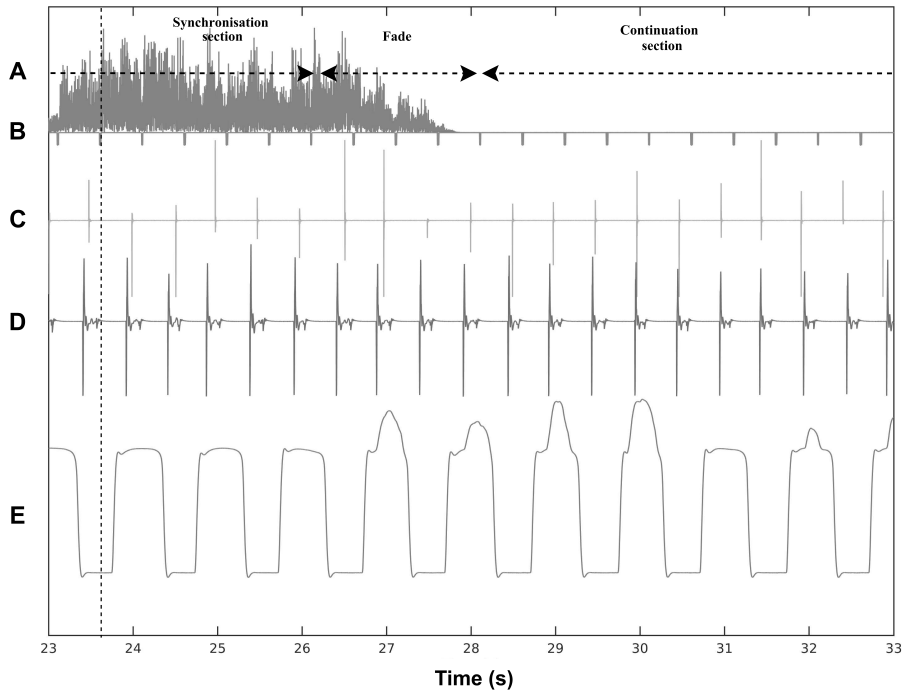
When all the equipment was appropriately fitted, the participant was invited to sit for a few minutes in total silence and to relax. A series of self-paced trials (i.e., without a pacing cue) was then executed in order to record each participant's SMT. The participant was asked to tap/walk at a regular pace for 90 s, at a tempo that seemed the most comfortable and natural to them. A total of two trials in each task (i.e., finger tapping, toe tapping, walking on the spot) were recorded.

After a short break of a few minutes, the three synchronisation–continuation tasks (i.e., finger tapping, foot tapping, stepping of the spot) were administered in a counterbalanced order across participants. For each task, the participant was required to (a) synchronise their movements with the auditory stimuli and (b) continue moving following the same regular tempo in silence. The synchronisation section was executed first for each experimental trial.

To optimise beat perception, the participant was instructed to listen to the two first bars of a priming metronome before initiating their movements. Then, the participant was instructed to synchronise their movements with the auditory stimuli for 10 bars (synchronisation section). When the stimuli ceased (fading period of one bar), the participant was instructed to continue tapping or stepping for a further 10 bars without auditory stimuli (continuation section; see Figure 19). The average duration of an experimental trial was 90 s. Following one practice trial in each task, a total of 18 trials was recorded (see Figure 20).

For each task, the participant was administered two auditory stimulus conditions (i.e., metronome beeps and musical excerpts). These two auditory stimulus conditions were composed of three trials each to enable random presentation of slow, medium, and fast tempi conditions (see Figure 20). Following each musical excerpt condition, the participant was asked whether they were familiar with the musical

Figure 19
Example of a 10-s Sample of the Auditive Stimuli and the Different Measured Variables



Note. Panel A: Sound spectrum. Panel B: Beat position. Panel C: Finger-tapping data. Panel D: Foot-tapping data, Panel E: Stepping-on-the-spot data (right foot).

excerpt (3-point familiarity scale, either 2 [*familiar*], 1 [*not sure*], or 0 [*unfamiliar*]), and how much they liked it (9-point Likert likability scale, ranging from 1 [*not at all*] to 9 [*a lot*]).

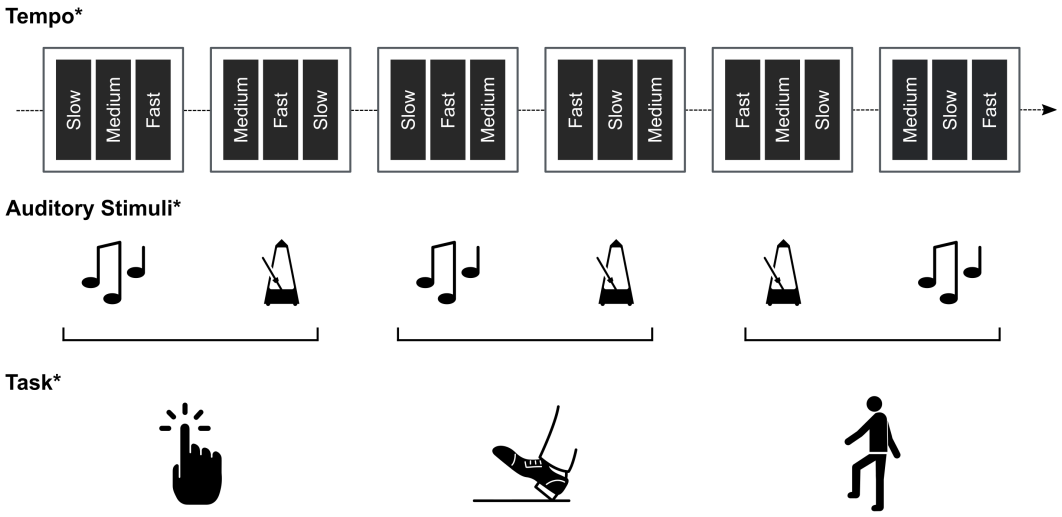
Between the tasks, the participant completed the Beat Alignment Test (Musil et al., 2021) and the Goldsmiths Musical Sophistication Index (Müllensiefen et al., 2014) to screen for group differences in relation to beat perception ability, musical training, and active engagement with music. The total duration of the experimental session was ~90 min.

5.2.3 *Task Description and Equipment*

In the finger- and foot-tapping tasks, the participant was seated comfortably on a chair in front of a table. A stomp box (Acoustim8, Series 100 foot drum, UK; Figure 1, left) was used to record the pace of each participant's movements. A stomp box is a small box containing a contact microphone that is often used as a foot drum by musicians to create the sound percept of a bass drum. With a curved frontage, this piece of equipment offers a large and easy to access target zone. The equipment enabled older participants to perform easily the tapping tasks. The stomp box was

Figure 20

Diagrammatic Representation of the Experimental Design



Note. Icon sources: "Music" by Kokota, "Metronome" by Mohammad Iqbal, "Finger Tap" by Symbolon, "Stepping on Gum" by Vertigophase (modified version), and "Exercise" by Co-Effect Creative (modified version) from the Noun Project. * = randomisation.

placed either on the table or on the floor, depending whether they were undertaking the finger- or the foot-tapping task (see Figure 18, left and middle panels).

In the stepping-on-the-spot task, a MP150 Biopac system was used (Biopac Systems, Goleta, CA) to record the pace of participant's movements. The sampling frequency was set at 1000 Hz. Two heel and toe strike transducers (Model RX111) gathered press and release data specifically in the stepping-on-the-spot task. The heel and toe strike transducers were taped into place on the sole of the shoe. The correct placement for the heel transducer was established by observing wear on the shoes. The placement of the transducer was set on that specific area to capture a clear signal with weight transfer. A Velcro elasticated band was used to attach the BioNomadix amplifier (Model BN-TX STRK2-T) around the ankles (see Figure 18, right panel).

Click track versions of the auditory stimuli consisting in oscillating bursts were generated by Logic Pro (Apple, Cupertino, USA). They were streamed in sync with the auditory stimuli to the Biopac, but not to the headphones of the participants, and continued during the whole 24 bars including the continuation section. The click tracks provided the means to synchronise the pace of participant's movements with the auditory stimuli (see Figure 19).

The psychology software Superlab (Version 5; Cedrus Corporation, San Pedro, USA) was used to generate randomisation of the auditory stimuli and tempo conditions. Participants listened to the auditory stimuli via stereo-dynamic headphones (Studiospares 448740) at self-adjusted volume levels. A LG Flatron (Model L17108) screen was used to display instructions.

Table 5
Musical Stimuli

Song Title	Artist	Year of Release	Tempi Class	BPM	IBI
Moments In Love[a]	Art of Noise	1984	Slow	69	870
Teardrop	Massive Attack	1998	Slow	77	779
El Condor Pasa	Leo Rojas	2012	Slow	81	741
Bitter Sweet Symphony	The Verve	1997	Slow	85	706
España Cañi[a]	Pascual Marquina Narro	1923[b]	Medium	120	500
Robot Rock	Daft Punk	2005	Medium	112	536
Axel F	Harold Faltermeyer	1984	Medium	117	513
March Of Toreadors From Carmen	Georges Bizet	1875[c]	Medium	120	500
Get Ready For This[a]	2 Unlimited	1991	Fast	125	480
Material Girl	Madonna	1984	Fast	136	441
Beat It	Michael Jackson	1983	Fast	139	432
Beautiful People	Marilyn Manson	1996	Fast	144	417

Note. BPM = beats per minute; IBI = inter-beat interval. [a]Used for practice trial only. [b]Recording in 2010. [c]Recording in 2011.

5.2.4 *Auditory Stimuli*

The auditory stimuli were created using the Logic Pro software. Pilot testing (N = 50 college students) established from 28 instrumental musical excerpts those which were considered easy to tap along (i.e., providing clear beats). Nine excerpts were chosen to represent three groups of tempi (slow, medium, and fast; Table 5). The metronome tracks were created to provide a selection of nine pacing stimuli that matched the pacing rates of those observed in the musical excerpts. The metronome sound used was the standard Klopfgeist tone from LogicPro, presented for 100 ms duration.

5.2.5 *Signal Preprocessing*

The acquisition files recorded by the Biopac MP150 were imported under Matlab and analysed with custom scripts to perform the automatic detection of the stimuli beats, finger/foot taps, and heel strikes.

5.2.5.1 *Extracting the Onsets of Finger and Foot Tapping*

A trend can be observed if a participant rested their hand or foot on the stomp box while performing the task. Hence, trends in the signal were first identified and removed by applying a zero-phase second-order Butterworth low-pass filter, with a cut-off frequency of 15 Hz. Thereafter, the absolute value of the detrended signal was low-pass filtered to compute an envelope (i.e., smooth curve outlining the extremes of the signal).

A coarse detection of the temporal onset of the taps was performed with a threshold set to five times the mean value of the envelope, within a 5-s sliding window. For each detected coarse onset, precise position in time was obtained by automatic

searching of the next sample for which the rectified signal went above the set threshold chosen to be 10 times the median value of the whole rectified signal.

5.2.5.2 *Extracting the Onsets of Stepping on the Spot*

The signal from each sensor ranged from 0 (when completely depressed) to 10 V (when fully pressed). As the participants had different gait patterns, force signals varied significantly from one individual to another. With some participants putting more emphasis on their heels and others on their toes, the data were aggregated from the two sensors. The right foot was used for subsequent analyses since the variation of the data was more pronounced, probably because all participants were right-handed.

A first rough detection of stomps was performed by searching the position at which the aggregated signal increased above 1 V. A more accurate location of the stomps was then performed by searching for the next sample for which the signal increased with the greatest slope. This position in time corresponded with the moment at which the participants exerted the most force with the foot and thus, the moment at which the participants wanted to project the beat.

For both the tapping and the stepping data, a Matlab script was written to offer a visual inspection of the events detected with the automatic algorithms. Visual inspection was performed to remove those automatically-detected taps that do not correspond to actual taps (i.e., false detections). During this visual inspection, false detections were identified from the shape of participants' taps. False detections were removed manually (< 12% of the trials).

5.2.6 *Measured Variables*

The IRI_{error}, asynchrony, and coefficient of variation were considered to examine the motor timing abilities of the participants as a function of the task (finger tapping, foot tapping, stepping on the spot), section (synchronisation, continuation), tempo (slow, medium, fast), and auditory stimuli conditions (metronome, musical excerpt). A glossary of terms is presented in Table 6.

5.2.6.1 *Entrainment to Produce Regular Time Intervals*

The IRI refers to the time interval between the onsets of two successive movements. This is the parameter commonly used in the tapping literature (see Repp, 2005, for a review). The production of an IRI sequence is based on the ability to retrieve a predefined time interval in working memory and produce repetitive movements following this specific pace. Three parameters can be used to characterise entrainment: the IRI_{error}, $|IRI_{error}|$, and CoV.

For each trial, each time series were first checked to detect and remove the IRIs greater than $1.7 \times IRI_{median}$ (i.e., omitted tap). The accuracy of time production was calculated as the relative error in IRI production following Equation 8:

$$IRI_{error} = \frac{IRI - ISI}{ISI} \times 100 \tag{8}$$

Table 6
Glossary of Terms

Acronym	Description
IRI_{error}	Measure of entrainment accuracy expressed as a percentage
$\lvert IRI_{error} \rvert$	Absolute IRI_{error} expressed as a percentage
CoV	Coefficient of variation indicating within-subject variability of entrainment (i.e., stability of performance in relation to the target interval)
ASYNC	Measure of synchronisation accuracy expressed in ms
|ASYNC|	Absolute ASYNC expressed in ms
ACoV	Coefficient of variation indicating within-subject variability of synchronisation (i.e., stability of performance in relation to the target beat)

A negative IRI_{error} indicated that the produced interval was too short compared to the targeted time interval (i.e., ISI). To gain an idea of the overall extent of production error, the IRI_{error} means were also calculated in absolute terms.

IRIs were also used to compute the coefficient of variation (CoV), which was considered to be an indicator of within-subject variability in motor production (i.e., performance stability; see Wilquin et al., 2018). For each trial, CoV was calculated using Equation 9:

$$\text{CoV} = \frac{SD_{\text{IRI}}}{M_{\text{IRI}}} \times 100 \tag{9}$$

5.2.6.2 *Synchronisation of Self-Initiated Actions to External Events*

SMS between self-initiated movements and external events is made possible though the predictability of the external event, arising from its recurrence. Three parameters can be used to characterise synchronisation performances: ASYNC, |ASYNC|, and ACoV.

For each trial, the accuracy of SMS was calculated as the time difference between the strike and the closest beat (Equation 10). ASYNCH were negative when the strike preceded the targeted beat.

$$\text{ASYNC} = \text{Strike}_{\text{start}} - \text{Beat}_{\text{start}} \tag{10}$$

To examine the error amplitude independently of error direction, the absolute ASYNCH was also calculated.

In addition, the asynchrony coefficient of variation (ACoV) was computed as an indicator of within-subject variability in SMS performance. For each trial, ACoV was calculated using Equation 11:

$$\text{ACoV} = \frac{SD_{\text{ASYNC}}}{M_{\text{ASYNC}}} \times 100 \tag{11}$$

5.2.7 *Statistical Analyses*

A trial was removed from further analyses if its (a) CoV was > 40% (Repp, 2003) and (b) ACoV was > 25% (Sowiński & Dalla Bella, 2013). In addition, trials were not included in further analyses if fewer than 18 and more than 44 strikes were recorded, due to participant error and/or equipment failure. These three criteria resulted in a loss of 4.3% data (28 trials from a total of 648 trials; 18 in the older group, and 10 in the younger group).

A multifactorial RM ANOVA (Section [synchronisation, continuation] × Task [finger tapping, foot tapping, stepping on the spot] × Auditory Stimuli [metronome, musical excerpt] × Tempo [slow, medium, fast]) was applied, with group (young, older) as a between group factor. An additional mixed-model RM ANOVA (Task [finger tapping, foot tapping, stepping on the spot] × Group [young, older]) was applied to the spontaneous motor tempo data.

Statistica (v.13.1) was used for the statistical analyses. Bonferroni corrections were applied to correct α for multiple comparisons. Normality was checked using the Shapiro–Wilk test. Where Mauchly's tests indicated violations of the sphericity assumption, Greenhouse–Geisser corrections were applied. Tukey post hoc tests were used where necessary.

5.3 RESULTS

5.3.1 *Beat Perception, Music Expertise, and Musical Preferences*

Results are presented in Table 7. For the Beat Alignment Test, there was an absence of group effect ($p > .50$), with the younger group characterised by slightly (but not significantly) less accurate performances ($M = 10.61$, $SD = 1.61$) than the older group ($M = 11.00$, $SD = 2.34$). For the Goldsmiths Musical Sophistication Index, a majority of participants ($n = 31$; 86.1%) reported learning a musical instrument at some stage (only two in adulthood, the rest between the ages of 4 and 15 years). No significant between-group differences were observed for the general Goldsmiths Musical Sophistication Index score ($p > .10$), and the musical training ($p > .40$) and active engagement subscales ($p = .070$). However, a significant effect of group was observed for musical genre preference, $F(1, 35) = 8.84$, $p = .005$. In the younger group, 15 (83.3%) participants preferred Rock/Pop, two (11.1%) preferred Classical, and one (5.6%) preferred Jazz. In the older group, seven (38.9%) participants preferred Rock/Pop, five (27.8%) preferred Classical, and six (33.3%) preferred Jazz.

5.3.2 *Spontaneous Motor Tempo*

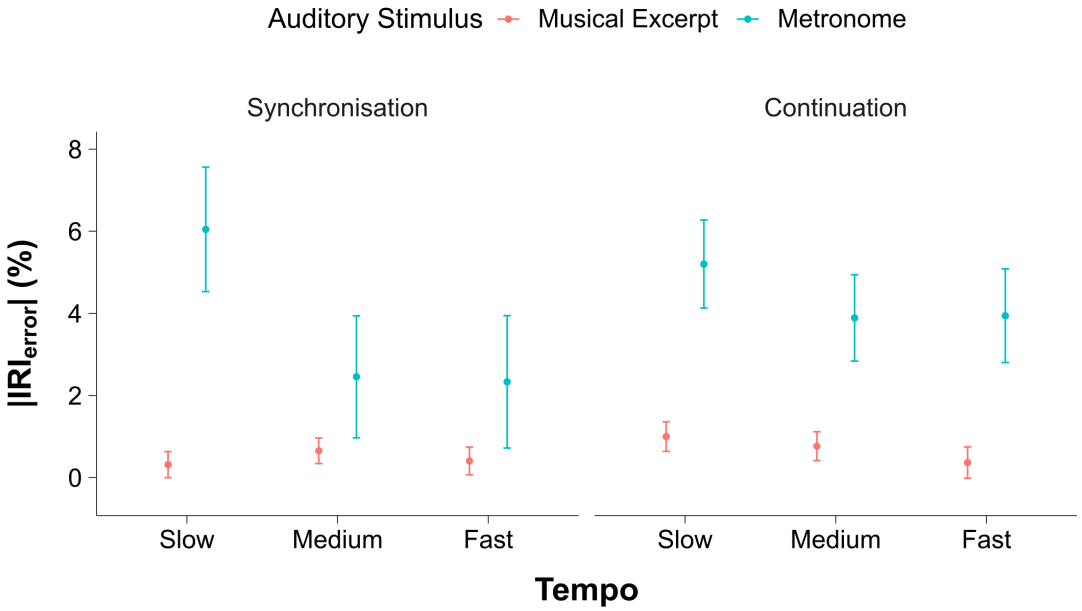
The RM ANOVA did not show a significant main effect of task, $F(2, 62) = 1.02$, $p = .367$, $\eta_p^2 = .03$, with SMT of 582 ($SD = 24$), 551 ($SD = 23$), and 571 ms ($SD = 20$) during the finger-tapping, foot-tapping, and stepping-on-the-spot tasks, respectively. The main effect of group was also non-significant, $F(1, 31) = 2.11$, $p = .156$, $\eta_p^2 = .06$, indicating that the SMT were similar in the younger ($M = 595$ ms, $SD = 26$) and older groups of participants ($M = 541$ ms, $SD = 28$). In the present findings, the mean

Table 7
Mean score of the Goldsmiths Beat Alignment Test and Musical Sophistication Index

	Younger			Older			Gold MSI Population Norms[a]			
Scores	*M*	*SD*	Range	*M*	*SD*	Range	*M*	*SD*	Range	Conbach's α
Beat Alignment Test	10.66	1.43	8–14	11.31	2.59	6–16	11.98	2.80	8.5–17	.67
Music Sophistication Index										
General	69.78	15.58	35–99	68.96	22.57	31–114	81.58	20.62	18–126	.93
Musical Training Subscale	19.75	8.27	7–36	21.54	12.37	7–43	26.52	11.44	7–49	.90
Active Engagement Subscale	36.50	9.41	18–53	34.38	11.85	15–57	41.52	10.36	9–63	.87

Note. Data are given for the two experimental groups and population norms. [a]Data provided from Musil et al. (2021).

Figure 21
Entrainment to the Pace of Regular Time Intervals



Note. Mean $|IRI_{error}|$ in % for each designated tempo, section, and auditory stimulus. Standard errors are represented in the figure by error bars attached to each mean point.

SMT of participants was 565 ms, which was not significantly different from medium tempo of auditory stimuli (i.e., 520 ms).

5.3.3 *Motor Timing Accuracy*

Only the significant main effects that are not related to an interaction are reported in the main body. Nonetheless, the statistics pertaining to each main effect are presented in Table 8.

Table 8
Statistical Analyses for Each Mean Effect and Significant Interactions

	df	*F*	*p*	η_p^2
$\lvert IRI_{error} \rvert$				
Tempo	2, 82	4.01	**.021**	.09
Auditory Stimuli	1, 82	79.26	**.001**	.49
Task	2, 64	0.65	.523	< .01
Section	1, 82	5.62	**.020**	.06
Group	1, 82	1.95	.167	.02
Tempo × Section × Auditory Stimulus	2, 82	5.73	**.005**	.14
IRI_{error}				
Tempo	2, 82	8.20	**.001**	.17
Section	1, 82	19.34	**.001**	.19
Tempo × Group	2, 82	3.15	**.048**	.07
Tempo × Auditory Stimuli	2, 82	8.13	**.001**	.17
CoV				
Tempo	2, 82	23.71	**.001**	.37
Auditory Stimuli	1, 82	3.62	.061	.04
Task	2, 82	91.96	**.001**	.53
Section	1, 164	0.53	.470	.01
Group	1, 82	1.53	.220	.02
Auditory Stimuli × Group	1, 82	5.16	**.026**	.06
|ASYNCH|				
Tempo	2, 62	7.95	**.001**	.20
Auditory Stimuli	1, 62	11.29	**.001**	.15
Group	1, 62	0.29	.592	.01
Auditory Stimuli × Task	2, 124	3.72	**.027**	.06
ASYNCH				
Tempo	2, 72	13.22	**.001**	.27
Task	2, 144	94.01	**.001**	.57
Group	1, 172	4.56	**.036**	.06
Auditory Stimuli × Task	2, 144	6.60	**.001**	.08
ACoV				
Tempo	2, 82	14.16	**.001**	.26
Auditory Stimuli	1, 82	6.72	**.011**	.08
Task	2, 164	0.59	.553	< .01
Group	1, 82	0.13	.717	< .01

Note. df = degrees of freedom.

Figure 22
Signed Entrainment to the Pace of Regular Time Intervals

Note. Mean IRI_{error} in % for each designated tempo and group. Standard errors are represented in the figure by the error bars attached to each mean point.

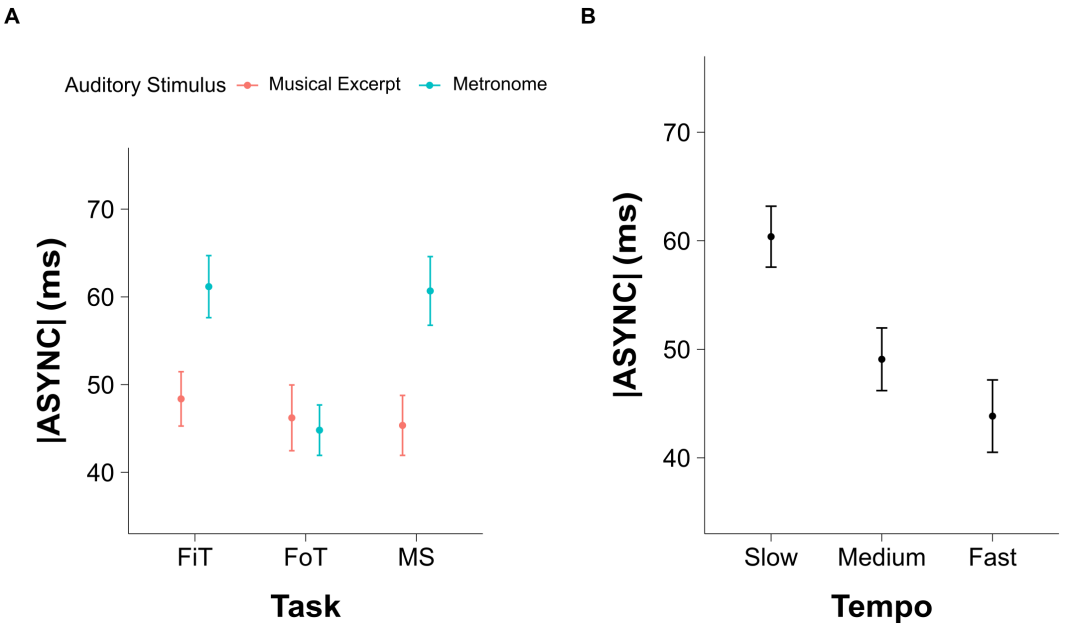
5.3.3.1 *Inter-Response Intervals*

The RM ANOVA conducted on the $|IRI_{error}|$ showed a significant Auditory Stimulus × Tempo × Section interaction was found, $F(2, 82) = 5.73$, $p = .005$, $\eta_p^2 = .14$. This indicated that, in the synchronisation section, $|IRI_{error}|$ means were similar across tempi when the auditory stimulus was a musical excerpt (M_{slow} = 0.3%, SD_{slow} = 0.3, M_{medium} = 0.6%, SD_{medium} = 0.3, M_{fast} = 0.4%, SD_{fast} = 1.6), but that errors were greater in slow (M = 5.4%, SD = 1.5) than in medium (M = 2.5%, SD = 1.5) and fast tempi (M = 2.3%, SD = 1.6) when the auditory stimulus was a metronome. In the continuation section, $|IRI_{error}|$ means remained significantly smaller when the auditory stimulus was a musical excerpt. The $|IRI_{error}|$ means were significantly greater in continuation than in synchronisation during the medium ($M_{synchro}$ = 2.5%, $SD_{synchro}$ = 1.5, M_{conti} = 3.9%, SD_{conti} = 1.1) and fast tempi trials ($M_{synchro}$ = 2.3%, $SD_{synchro}$ = 1.6, M_{conti} = 3.9%, SD_{conti} = 1.1) but only when the auditory stimuli was a metronome (see Figure 21).

The RM ANOVA conducted on the IRI_{error} showed a significant main effect of section, $F(1, 82) = 19.34$, $p = .001$, $\eta_p^2 = .19$, indicating that IRI_{error} were negative (i.e., too short IRI) in the synchronisation section but positive (i.e., too long IRI) in the continuation section. The Group × Tempo interaction was significant, $F(2, 82) = 3.15$, $p = .048$, $\eta_p^2 = .07$, with an absence of group difference only in the medium tempo class. Nonetheless, IRI_{error} means were more negative in the older than in the younger group during the slow tempo trials (M_{older} = -2.6%, SD_{older} = 0.6, $M_{younger}$ = -0.8%,

Figure 23

Synchronisation of Self-Initiated Actions to External Predictable Events



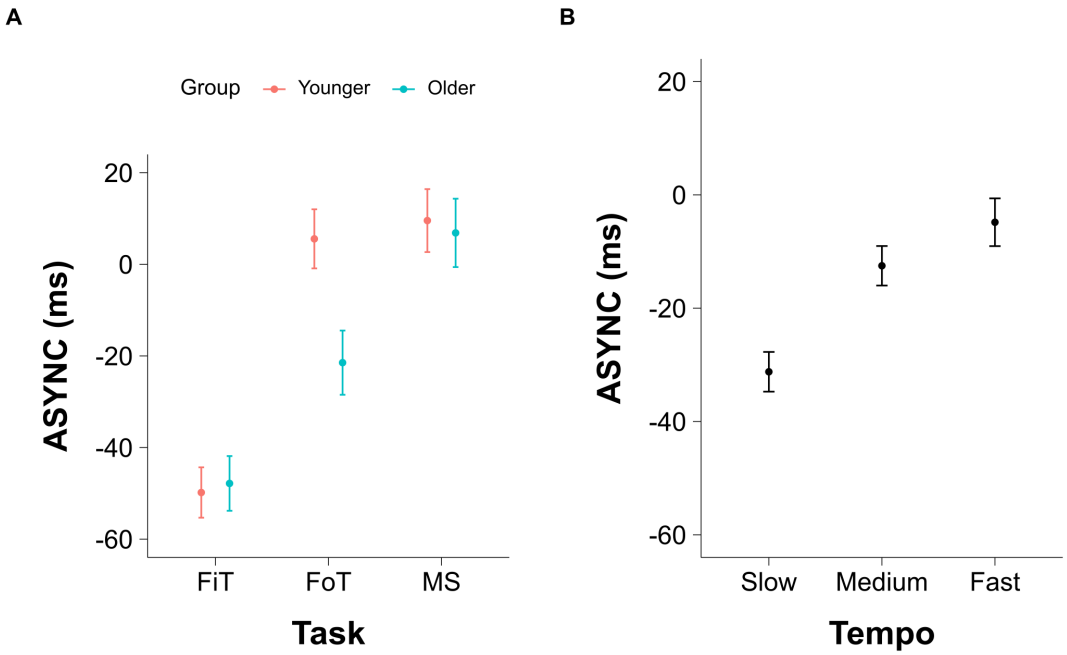
Note. Panel A: Mean |ASYNCH| in ms for each designated auditory stimulus and task. Panel B: Mean |ASYNCH| in ms for each designated tempo. Standard errors are represented in the figure by the error bars attached to each mean point. FiT = finger tapping, FoT = foot tapping, MS = marching on the spot.

$SD_{younger}$ = 0.5) and more positive during the fast tempi trials (M_{older} = 1.2%, SD_{older} = 0.7, $M_{younger}$ = 0.4%, $SD_{younger}$ 0.6) (see Figure 22). A significant Auditory Stimulus × Tempo interaction was also found, $F(2, 82) = 8.128$, $p = .001$, $\eta_p^2 = .17$, with similar IRI_{error} across tempi when the auditory stimulus was a musical excerpt. When the auditory stimulus was a metronome, negative (M = -3.1%, SD = 1.9) and positive IRI_{error} (M = 1.4%, SD = 2.0) were observed for slow and fast trials, respectively.

The RM ANOVA conducted on the CoV showed a significant main effect of tempo, $F(2, 82) = 23.71$, $p = .001$, $\eta_p^2 = .37$, with larger CoV in slow (M = 36.7%, SD = 1.6) than in medium (M = 25.9%, SD = 1.5) and fast tempi (M = 21.5%, SD = 1.7). The main effect of task was also significant, $F(2, 82) = 91.96$, $p = .001$, $\eta_p^2 = .53$, indicating that CoV was larger during the finger (M = 30.8%, SD = 2.1) and foot-tapping task (M = 34.1%, SD = 2.6) than in the stepping-on-the-spot task (M = 19.3%, SD = 2.0). The Group × Auditory Stimulus interaction was significant, $F(1, 82) = 5.16$, $p = .026$, $\eta_p^2 = .06$, with greater CoV in the metronome (M = 28.4%, SD = 3.5) than musical excerpt condition (M = 25.4%, SD = 3.8) in the older group. Nonetheless, similar CoV was observed in the metronome (M = 29.1%, SD = 3.0) and musical excerpt conditions (M = 29.3%, SD = 3.3) for the younger group.

Figure 24

Signed Synchronisation of Self-Initiated Actions to External Predictable Events



Note. Panel A: Mean ASYNCH in ms for each designated group and task. Panel B: Mean ASYNCH in ms for each designated tempo. Standard errors are represented in the figure by the error bars attached to each mean point. FiT = finger tapping, FoT = foot tapping, MS = marching on the spot.

5.3.3.2 *Asynchrony*

The RM ANOVA conducted on the |ASYNCH| showed a significant main effect of tempo, $F(2, 62) = 7.95$, $p = .001$, $\eta_p^2 = .20$, indicating smaller |ASYNCH| in fast (M = 43.8 ms, SD = 3.3) vs. slow tempi (M = 60.3 ms, SD = 2.8; see Figure 23). The Auditory Stimuli × Task interaction was significant, $F(2, 124) = 3.72$, $p = .027$, $\eta_p^2 = .06$, indicating that in the finger-tapping and the stepping-on-the-spot tasks, the |ASYNCH| was significantly smaller when the auditory stimulus was a song (M_{finger} = 48.4 ms, SD_{finger} = 3.1, $M_{marching}$ = 45.4 ms, $SD_{marching}$ = 3.4) rather than a metronome (M_{finger} = 61.2 ms, SD_{finger} = 3.5, $M_{marching}$ = 60.7 ms, $SD_{marching}$ = 3.91). |ASYNCH| was similar in both auditory stimuli when participants performed the foot-tapping task (see Figure 23).

The RM ANOVA conducted on the ASYNCH showed a significant main effect of tempo, $F(2, 72) = 13.22$, $p < .001$, $\eta_p^2 = .27$, with larger negative ASYNCH in the slow (M = -31.2 ms, SD = 3.5) than in the medium (M = -12.5 ms, SD = 3.5) and fast tempi trials (M = -4.8 ms, SD = 4.2). The Group × Task interaction was significant, $F(2, 144) = 6.60$, $p = .001$, $\eta_p^2 = .08$, indicating that the ASYNCH was negative in the finger-tapping task (M = -48.8 ms, SD = 5.6) and positive in the stepping-on-the-spot task (M = 7.9 ms, SD = 7.1) in both the young and older groups of participants (see

Figure 24). In the foot-tapping task, the ASYNCH was positive for the younger group (M = 9.6 ms, SD = 6.8) and negative in the older group (M = -21.5 ms, SD = 7.0).

The RM ANOVA conducted on the ACoV showed a significant main effect of tempo, $F(2, 82) = 14.16$, $p = .001$, $\eta_p^2 = .26$, with larger ACoV in the slow (M = 38.4%, SD = 1.8) than in the medium (M = 29.6%, SD = 1.8) and fast trials (M = 24.4%, SD = 1.9). The main effect of auditory stimulus was also significant, $F(1, 82) = 6.72$, $p = .011$, $\eta_p^2 = .08$, indicating that ACoV was smaller in the musical excerpt (M = 29.0%, SD = 2.1) than in the metronome trials (M = 32.6%, SD = 2.3).

5.4 DISCUSSION

The main purpose of the present study was to examine timing performance during the execution of motor behaviours varying in ecological validity (i.e., finger tapping, foot tapping, marching on the spot). Two types of auditory stimuli (i.e., metronome, musical excerpt) were used as cues to perform the three synchronisation–continuation tasks at fast, medium, and slow paces. H_1 was verified as performing the tasks at SMT led to better timing performance than moving faster or slower. Synchronisation performances were better during stepping on the spot and finger tapping when compared to foot tapping; hence, H_2 was only partially verified. H_3 was confirmed since performing the SMS tasks with musical excerpt led to higher timing performances than with metronome. Timing performances were overall better in the young than in the older participants; thus, H_4 was verified.

Entrainment is defined as the temporal alignment of movements with the pace of a regular cue without specifically synchronising each motor element to a discrete time point (Wilquin et al., 2018). This phenomenon has been proposed to emerge though the auditory–motor feedback/forward loops in which the regularity of events are encoded to assist motor production (see Thaut et al., 2015). In contrast, synchronisation is a cognitive skill that can be further trained (as observed in studies of superior performance in dancers and musicians; Karpati et al., 2016; Repp & Su, 2013) to intentionally and accurately coordinate self-initiated actions with pacing cues. The findings reported in the present study provide a direct comparison between synchronisation and entrainment processes as a function of both the complexity of body movements and nature of the pacing cues.

5.4.1 *Complexity of Body Movements*

Collectively, the findings of the present study showed that timing abilities were better during the whole-body stepping task when compared to the finger and foot-tapping conditions. In timing research, the finger-tapping task has been extensively used to examine and model the motor timing abilities of humans. Nonetheless, the results reported in the present study suggest that whole-body (i.e., stepping on the spot) and single-limb (i.e., finger or foot) movements may not be underpinned by the same timing control mechanisms. These findings demonstrate the importance of developing sensorimotor tasks using whole-body movements for a better understanding of motor timing in daily life situations.

While both stepping on the spot and finger tapping afforded better synchronisation performances than foot tapping, these two tasks were characterised with contrasting error directions. More precisely, negative and positive mean asynchronies were observed in the tapping and stepping task, respectively. These findings are consistent with those reported by other studies using whole-body stepping movements (Khan et al., 2020). Schaal et al. (2004) differentiated between discrete and continuous movements based on the nature of the errors made in sequential motor timing. They proposed that rhythmic movements such as walking and scratching are "phylogenetically old motor behaviours" (p. 1137) found in many organisms. By contrast, discrete movements (e.g., reaching and tapping) involve higher order cortical planning.

Tapping in synchrony with a beat requires anticipatory mechanisms (Aschersleben et al., 2001; Stenneken et al., 2006) and may depend on a predictive timing mode. By contrast, stepping on the spot is a dynamical (continuous) task that would rely on emergent timing (see e.g., Delignieres & Torre, 2011; Pressing, 1999; Repp & Steinman, 2010). This interpretation is congruent with the present findings indicating that tapping produces typical negative mean asynchronies, whereas the stepping on the spot task produces positive asynchronies.

5.4.2 *Music vs. Metronome*

An important results of the present study is that the musical excerpt condition enabled better entrainment than the atonal metronome beats, both during the synchronisation and continuation phases. The concept of rhythmic entrainment is often described in terms of embedded hierarchies such as beat-simple/beat-complex, metre, syncopation, pulse, and periodicity (Levitin et al., 2018). Nonetheless, this does not preclude other perceptual groupings of sounds (Iversen et al., 2008). Music is a complex series of temporal auditory events. The sound envelope presented to the participants included multiple levels of rhythmic, but also melodic musical factors, described as motifs, hooks, or riffs in popular music. A plausible hypothesis is that such a richness in the sound envelope allow to guide motor production to a greater extent than a simple beep.

In contrast to the metronome condition, when moving to music, participants maintained similar levels of timing performances during the continuation and the synchronisation sections. Musical excerpts did not contain words/lyrics that could have artificially impacted the participants' mood or semantic memory. Nevertheless, Jakubowski et al. (2015) have provided evidence that during the recall of familiar and imagined music, memory for tempi is constant and veridical (maximal deviation of 17.3% from the original). The mental representations of sounds may facilitate motor prediction in the musical excerpt condition and thus, movement planning in respect to future events.

While clear and controlled, the metronome stimulus is inferior to music in terms of providing an auditory guidance to motor production. This may be particularly important for interventions using auditory cues for movements, such as in the neurorehabiliation of people with Parkinson's disease. Rose et al. (2019) reported that music enabled people with Parkinson's disease to perform movements as well as healthy controls, which was not the case for metronome. Anecdotally, patients de-

scribed that the metronome ticks were "like a shadow" that was easy to get lost in. In contrast, the music provided something more tangible that the patients could either subvocalise or sing out loud during the continuation section to maintain the pacing of their movements. The results of the present study extant those findings by showing that music contains more useful sonic information than metronomes alone for healthy participants across ages.

5.4.3 *The Pace of Motor Execution*

As predicted, motor timing was more accurate and stable when the motor tasks were performed at the medium tempi in comparison to fast and slow tempi. The timing performance of the participants suffered when the pacing was fast, indicating that the task was reaching the limits of the sensorimotor loops needed to correct motor production errors. Notably, performance losses were the most significant for the slower tempo, both in terms of synchronisation and pacing stability – even if participants had time to monitor spatial and timing errors.

In relation to predictive timing theories, the rate limits of the slower tempi in the present study were not below those inducing distortions in the subjective present (Wittmann et al., 2011). Nonetheless, the ability to synchronise movements with slow tempi required the maintenance in working memory of the time interval that was to be performed. The extraction of memory traces to guide rhythmic-motor output is a complex process that gives rise to errors and entails a significant cognitive cost (Guérin et al., 2021a). Even if counter intuitive, the present experimental findings have been recently confirmed by biological models showing that motor timing is more accurate in fast than in slow tempo (Hardy et al., 2018).

5.4.4 *Limitations and Future Directions*

To resonate in both the timing-research community and applied therapeutic applications, one limitation of the present study is the necessity for replication. More trials should be conducted whereby the concepts of musical affect and familiarity are closely considered. For example, music can also be used to enhance positive and reduce negative affective states (Karageorghis, 2020; MacDonald, 2013). In addition, future studies could consider the use of self-selected music matched to participants' individual spontaneous motor tempo in comparison to a set of pre-chosen musical excerpts.

5.4.5 *Conclusions*

The findings of this chapter showed that whole-body movements are characterised by fewer timings errors and less variability than single-limb movements. Finger tapping is a good laboratory-set task. However, tapping-to-metronome paradigms are too far removed from natural behaviours to facilitate direct application of the findings. Future researchers need to give careful considerations to the substitution of traditional laboratory tasks involving single-limb movements with more ecological motor tasks in order to optimise reliability and generalisability of their findings.

INTERMEDIATE SUMMARY

Finger-tapping tasks are classically used in the scientific literature to investigate sensorimotor synchronisation abilities in relation to neutral auditory cues, such as metronomes. However, music is more commonly associated with an entrained bodily response, such as foot tapping and dancing. The general aim of Chapter 5 was to examine the effects of metronome and musical auditory stimuli on motor timing abilities across the three motor tasks varying in ecological validity (i.e., finger tapping, foot tapping, stepping on the spot). The auditory stimuli were presented at slow, medium, and fast tempi.

The findings suggested that the task of stepping on the spot enabled better timing performances than finger and foot tapping both in young and older adults. Timing performances followed an inverse U shape, with best performances observed in the medium tempi that were set close to the spontaneous motor tempo in each movement type. In addition, music provided an entrainment effect that enabled better performances and greater stability than classically reported using a metronome.

Chapter 5 has been published in *Scientific Reports* (2021). In addition, the results have been the subject of one conference presentations (2020, 15e Journée Scientifiques des Jeunes Chercheurs, Lille, France). It also inspired a contribution in *The Conversation*.

Using laboratory-based tasks that consist of artificial upper-limb movements, behavioural studies showed that the production of fast and slow movements entailed two different processes (i.e., automatic vs. controlled). Nonetheless, single-limb and whole-body movements were found to engage different timing modes that might affect the way temporal control is applied over motor behaviours. The general aim of Chapter 6 was to examine prefrontal and motor activity during the execution of both a continuous finger and stepping task varying in motor pace.

6

EFFECTS OF MOTOR PACE ON FRONTAL ACTIVITY DURING WHOLE-BODY MOVEMENTS

Submitted for publication as Guérin, S. M. R., Vincent, M. A., & Delevoye-Turrell, Y. N. (2021b). Effects of motor pacing on frontal-haemodynamic responses during continuous finger and whole-body movements. Manuscript submitted for publication.

6.1 INTRODUCTION

Locomotion is a fundamental behaviour that consists in a robust motor pattern repeated over time. Experimental evidence has indicated that human beings perform routine locomotion behaviour at ~2 Hz, which corresponds to two steps per second (MacDougall & Moore, 2005). This particular motor frequency has been referred to as the spontaneous motor tempo (Fraisse, 1982; Moelants, 2002). Nonetheless, individuals periodically need to accelerate or slow down the spontaneous pace of their actions in order to accommodate environmental constraints. For illustrative purposes, this is the case when trying not to miss a train or holding the hand of a toddler while walking down the street.

The way temporal control is applied over motor behaviours is still largely unknown. In the scientific literature, motor timing abilities have been commonly investigated using laboratory tasks that consist in artificial upper-limb movements (e.g., finger tapping; for a review, see Repp, 2005). Using this type of task, the production of fast motor behaviours was found to entail an automatic process in which the temporal regularities emerge from body dynamics (Lemoine, 2007; Lewis & Miall, 2003b). In contrast, the ability to perform slow movements may be underpinned by cognitive control (Bobin-Bègue & Provasi, 2008). More specifically, Bobin-Bègue et al. (2006) advocated that newborns and babies are unable to perform movements slower than their spontaneous pace because their motor inhibition function is not yet matured. These results corroborate our findings that motor production at slow pace led to higher cognitive cost when compared to voluntary actions executed at close-to-spontaneous and fast paces in the adult population (Guérin et al., 2021a).

Brain imaging has been efficiently used to highlight the involvement of motor inhibition during go/no-go tasks (see e.g., Albares et al., 2014; Levin et al., 2014; Rubia et al., 2001). These studies found that the dorsolateral prefrontal and orbitofrontal cortices play a key role in inhibiting motor actions by modulating the strength of communication between prefrontal and motor regions (Rae et al., 2015). The go/no-go paradigm is easily implemented during brain recordings as it requires simple finger-responses. Yet, it remains unclear whether the obtained results can be generalised to the timing of whole-body movements. Neuroimaging methods (i.e., EEG, *f*MRI) are indeed highly sensitive to motion artefacts, which renders challenging the recording of cerebral activation during whole-body motor tasks.

*f*NIRS is a neuroimaging technique that enables the monitoring of brain activity in whole-body movement paradigms (Leff et al., 2011; Perrey, 2014). *f*NIRS technology makes use of the neurovascular coupling (i.e., the relationship between neuronal activation and subsequent changes in cerebral blood flow; Pasley & Freeman, 2008) to infer the magnitude and spatial location of brain-cortical activity in response to experimental manipulations. In a previous study, we successfully used *f*NIRS to dissociate the involvement of different cognitive mechanisms as a function of task demands using a finger-tapping task (Guérin et al., 2021c). In addition, the haemodynamic responses recorded with *f*NIRS over the motor cortex were shown to be consistent with those reported using the same SMS tasks in *f*MRI (Rahimpour et al., 2020). Thus, *f*NIRS is a suitable tool to have a vista on the neurophysiological mechanisms involved in the pacing of whole-body movements.

The aim of the present study was to examine prefrontal and motor activity during the execution of continuous motor tasks at various tempo. Two tasks were used: a classic upper-limb task (i.e., drawing) and a whole-body stepping-on-the-spot task (i.e., steady-state walking). Despite being characterised by contrasting ecological value, the drawing and walking tasks both belong to the category of continuous movements, defined as having "no recognisable beginning and end" (Schmidt et al., 1988, p. 46). These two motor tasks were executed in SMS at fast (i.e., 300 ms), close-to-spontaneous (i.e., 600 ms), and slow paces (i.e., 1200 ms). Brain activity was recorded using the *f*NIRS technique over the bilateral primary motor and prefrontal cortices (i.e., orbitofrontal and dorsolateral regions) because of their involvement in inhibitory control.

It was hypothesised that steady-state walking will lead to a larger increase in cerebral oxygenation over the primary motor cortex when compared to drawing due to the necessity to control whole-body musculature (H_1). Performing movements at slow pace will lead to more prefrontal activation when compared to actions executed at close-to-spontaneous and fast paces (H_2). This effect would be magnified for movements that deeply ingrained in human brain circuitry (i.e., steady-state walking; H_3). In addition, during both tasks, the slow tempi trials will lead to less activity in the motor areas than close-to-spontaneous and fast tempi trials (H_4).

6.2 MATERIALS AND METHODS

6.2.1 *Participants*

Healthy adults were recruited for the present study among the staff and student corpus of the University of Lille. Inclusion criteria were normal to corrected-to-normal vision and the absence of motor dysfunctions and neurological/psychiatric disorders. Participants were informed of the tasks that they would need to perform at least 48 hr prior to inclusion. After reading the information sheet, each participant was invited to provide written informed consent. At this point, participants were considered to be included in the experiment and demographic data were collected (i.e., sex, age). The ethics committee of the University of Lille (France) approved the study (see Appendix A).

The sample size required for the present study was calculated using G*Power (3.1.9.2). The *f*NIRS results of Guérin et al. (2021c) were used as group parameters. The power analysis indicated that a total of 12 participants was required (f = .52; α = .05; 1-β = .80). Three additional participants were included to guard against deletions due to experimental outliers.

The small telescopes approach was applied to determine the SESOI (Simonsohn, 2015) for each hypothesis. Accordingly, the SESOI was set to the effect size that an earlier study would have had 33% power to detect (Lakens et al., 2018). Once again, the *f*NIRS results of Guérin et al. (2021c) were used. The sensitivity analysis indicated that an effect size of at least f = .27 (i.e., η_p^2 = .07) was required to yield meaningful results.

6.2.2 *Tasks Description and Materials*

6.2.2.1 *Experimental Procedure*

Participants were administered two motor tasks: (a) a drawing task on a touchscreen and (b) a steady-state walking task. The experimental session took place in a quiet, windowless room that was dimly lit. Lighting is of particular concern given that bright light can affect *f*NIRS signals (Shadgan et al., 2010).

For the drawing task, the touchscreen (1915L Elo IntelliTouch 19"; Elo Touch Solutions Inc.; Milpitas, California, CA) was placed on a table in front of the participant with the screen oriented at 45°. The participant was seated on a stool to minimise lower-limb muscular fatigue and avoid any extraneous movements during task performance. For the steady-walking task, the participant was asked to stand in the centre of the room.

The *f*NIRS system (FOIRE-3000/16; Shimadzu, Kyoto, Japan) was placed behind the participant to limit distraction and facilitate the management of the cables. The cables were supported by an adjustable mechanical stand to carry the weight of the optical fibres (Coyle et al., 2007). This setup provided a means by which to ensure rigid *f*NIRS cable positioning, but also to minimise participant's strain and discomfort. A self-rated pain scale was also administered at the beginning and end of the experimental session. The scale was attached to a 9-point Likert pain scale, ranging from 1 (*no pain*) to 9 (*unbearable pain*). The participant was required to indicate the degree of pain that was experiencing in regard to the weight of the optodes on the head and neck.

6.2.2.2 *Task Description*

The two motor tasks were administered in a counterbalanced order across participants. In the drawing task, six targets (dots of 10-mm diameter) positioned around a 100-mm circle were display on the screen. The participant was required to trace the circle clockwise using the index finger with a closed fist. The participant was instructed to maintain accuracy in both temporal and spatial facets of the skill, but to favour temporal accuracy in case the task became too challenging for both to be maintained. In the walking task, the participant was asked to walk on the spot.

The participant performed the drawing and steady-state walking tasks in synchrony with an auditory metronome set at three predefined tempi. The beeps of the metronome (duration = 80 ms, sound frequency = 294 Hz) were generated using Matlab 7.11.0 R2010 software (Mathworks Inc.; Natick, Massachusetts). When the beep sounded, the participant was required to have: (a) their index finger of the dominant hand placed on the relevant target for the drawing task; (b) one foot on the ground for the walking on the spot task. The participant was instructed to synchronise their right and left legs alternately during the walking task.

The three tempi used in the study were 300 (i.e., fast tempo), 600 (i.e., close to spontaneous motor tempo), and 1200 ms (i.e., slow tempo). The fast- and slow-tempo trials enabled the participant to depart from their spontaneous motor tempo but remain within the possible SMS zone (between 180 ms and 1800 ms; Keele et al., 1985; Mates et al., 1994). Two Creative SBS 250 desk speakers (Creative Technology; Singapore) were used to play the metronome beeps.

6.2.2.3 *Experimental Design*

A block design procedure (i.e., alternating periods of activity and respite) was used in the present study. Each trial lasted 40 s and was preceded by a rest period of 30 s to allow the haemodynamic indices to return to baseline levels. The participant was presented with six blocks of three trials and was instructed to perform the two visuomotor tasks while synchronising their movements to the metronome. Three blocks of trials were recorded for each task, with the slower, close-to-spontaneous, and faster conditions administered in a random order. Throughout the session, participants were encouraged not to speak and to avoid extraneous movements during each *f*NIRS trial. The total duration of the experimental test period was ~90 min.

6.2.3 *Data Acquisition and Preprocessing Analyses*

6.2.3.1 *Behavioural Data*

DRAWING TASK. Data were collected using the touchscreen. Radii from the centre of the circle to each target were computed. Points of interest were defined as the locus that intersects the participant's finger and each radius. IRIs were measured as the time interval between the onset of successive points of interest.

WALKING TASK. Data were collected using six Oqus 5+ cameras (Qualisys MoCap, Göteborg, Sweden). A spherical passive marker was taped to the right participant's shoe to follow the movement of the foot. The recorded data were Cartesian coordinates (i.e., x, y, and z) and the points of interest were defined as the local maximum of z coordinates. IRIs were measured as the time interval between the onset of successive points of interest. Each IRI value was divided by two because only the right foot position was recorded.

TIMING ACCURACY. Before conducting the main analyses, the time series was checked in order to detect and remove the IRI greater than twice the ISI of a given block of trials. These trials were referred to as temporal omissions and were not in-

cluded in further analyses. An IRI_{error} was computed as the percentage of absolute difference between an IRI and its reference ISI for a given time interval t (see Equation 4). The mean IRI_{error} measurement within a trial indicated the accuracy of time interval production (Repp, 2005).

6.2.3.2 *Headset Position Tracker*

The position of the *f*NIRS headset was recorded using six Oqus 5+ cameras (Qualisys MoCap, Göteborg, Sweden) in the course of the entire experimental session. Specifically, one spherical passive marker was taped to the participant's right temple and two markers to the headset. The position for each marker was given in Cartesian coordinates (i.e., x, y, and z). The spatial accuracy of the system was 0.02 mm for each dimension of 3D space.

To verify the occurrence of an *f*NIRS headset shift, the surface of the planar triangle connecting the 3D markers was computed over a 30-s timing window (a) 30 s after the beginning of the experimental session and (b) 30 s before the end (see Equation 1). The percentage of variation between the two values was then calculated. An *f*NIRS headset shift was detected if this value exceeded 15% (for a similar procedure, see Guérin et al., 2021c). If an *f*NIRS headset shift was detected, the behavioural and *f*NIRS data from the corresponding participant were removed prior to further analyses

6.2.3.3 *Cardiorespiratory Monitoring*

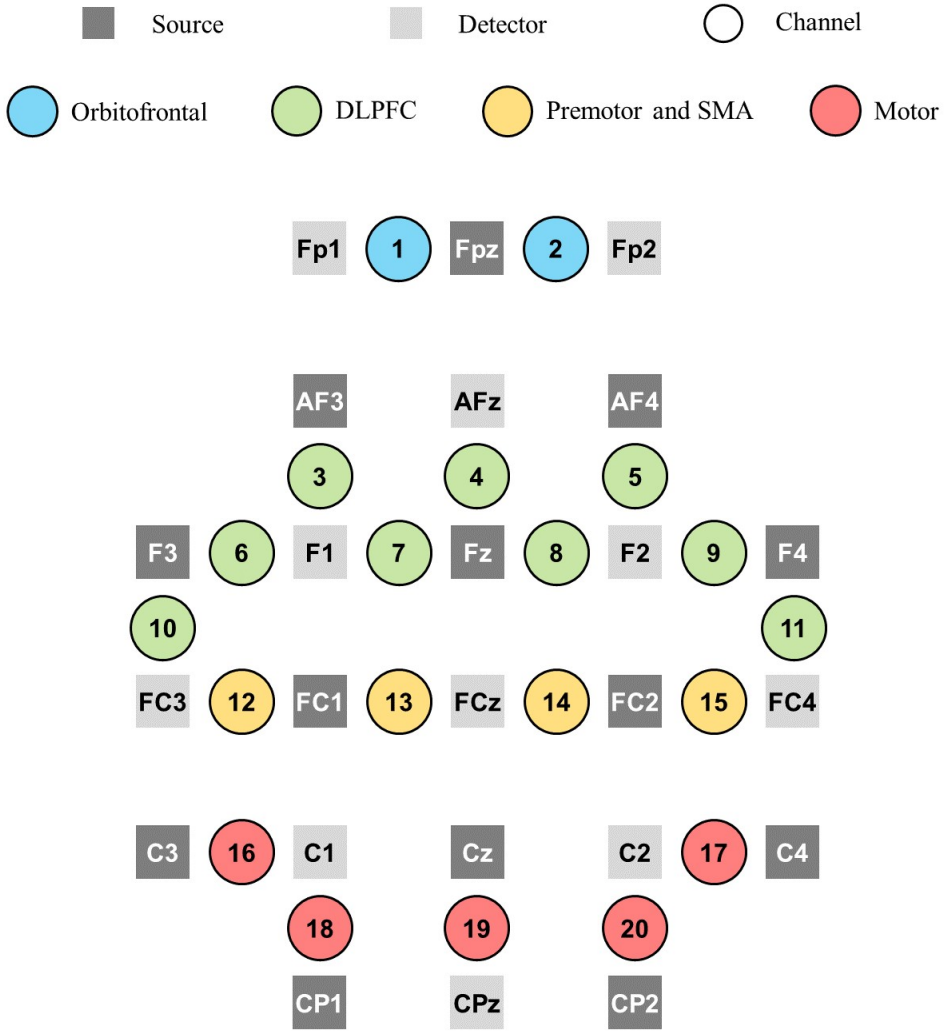
HR and respiration frequency were recorded to check the quality of the raw *f*NIRS signal (Pinti et al., 2019). Cardiorespiratory monitoring was conducted using an MP150 Biopac system (Biopac Systems, Goleta, CA), complemented with two dedicated add-on wearable devices. To facilitate acquisition, data were captured using a dual wireless respiration–electrocardiogram BioNomadix module. HR was captured by means of BN-EL45-LEAD3 lead set and two disposable patch electrodes placed on the participant's right and left clavicles. Respiration rate was recorded using a BN-RESP-XDCR respiration transducer. This respiratory belt was placed around the chest wall, below the sternum. The sampling frequency was set to 1000 Hz for both indices. Data acquisition was managed with the Acq*Knowledge* software.

6.2.3.4 *f*NIRS Data

DATA ACQUISITION. Data were collected using a continuous-wave *f*NIRS system operating at three near-infrared wavelenghts (780, 805, and 830 nm) and monitored by the associated LabNIRS software. The sampling frequency was set at 2.27 Hz (i.e., temporal resolution of 440 ms). HbO_2 and HHb (mMol/L*cm) were computed in real time using Equations 5 and 6 (generated by LabNIRS from the modified Beer-Lambert law; Baker et al., 2014).

The fOLD toolbox (*f*NIRS Optodes' Location Decider; Morais et al., 2018) was used to guide the selection of optimal optode positioning with respect to the brain regions of interest, which were the bilateral orbitofrontal cortex (Brodmann's area 10), dorsolateral prefrontal cortex (Brodmann's area 9), premotor cortex and SMA

Figure 25
Diagrammatic Representation of the Sources, Detectors, and Channel Layout



Note. DLPFC = dorsolateral prefrontal cortex; SMA = supplementary motor area.

(Brodmann's area 6), and primary motor cortex (Brodmann's area 4). Thus, a 20-channel (13 light sources [multicomponent glass bundle fibers], 11 detectors [multi-alkali photomultipliers detectors]) configuration was designed in order to ensure an anatomical specificity of at least 30% for each region of interest (see Figure 25).

The optodes were attached to an *f*NIRS headset with a 3-cm source-detector distance, giving a depth of analysis between 0.5–2.0 cm. The headset was placed on each participant's head in accord with the International 10–20 system guidelines for standard electrode positions (Jasper, 1958). As a result, the Cz optode was located at the midway point between the nasion and inion. A stylus with a LED light was used to spread the hair in each optode hole before the corresponding optode was wired

to the *f*NIRS headset. This is of particular importance to avoid light obstruction due to the presence of hair between the optode and participant's scalp.

System calibration was performed through an automatic adjustment using LabNIRS to adapt the internal parameters of the *f*NIRS device (e.g., gain, amount of light to emit) to the head morphology and the hair-type characteristics of each participant. Calibration was performed at the beginning of each experimental session. In case the amount of light detected was not sufficient, the hair was pushed back beneath each problematic source-detector couple.

DATA PROCESSING. To control for the quality of the acquired *f*NIRS data, the PSD was computed using the raw *f*NIRS intensities for each participant, trial, and channel. The frequency corresponding to maximal peak in the 50–160 beat-per-minute (bpm) range was detected visually. The identified frequencies were compared to the HR measurements provided by the Biopac system. A participant was removed from further analyses if HR frequency was not visible in the *f*NIRS signals. Nine participants were rejected on this basis. Note that any excluded participants were replaced to have a final sample size of $N = 15$.

The presence of the heart pulse is a necessary, but not sufficient condition to ensure the quality of *f*NIRS data. Thus, the QT-NIRS toolbox (Quality Testing of Near-Infrared Scans; Hernandez & Pollonini, 2020) was used to identify channels with poor optical coupling. More specifically, the scalp-coupling index was computed by use of the following parameters: cardiac filter = 0.5–2.27 Hz; time window = 5 s; λ = 805 and 830 nm.

The scalp-coupling index quantified the cross-correlation between the cardiac waveform of two wavelengths (i.e., 805 and 830 nm) for each channel over the entire trial (Pollonini et al., 2016). For a given participant and channel, trials with a scalp-coupling index < 0.8 were removed prior to further analyses (trial = 5 s baseline + 40 s task). Overall, 1.72% of the trials was removed in accord with this criterion. For each participant and task, the entire channel was removed if < 70% of the trials were ineligible. 1.88% of the channels pertaining to the brain region of interest was removed on this basis.

Correction for motion artefacts was performed using wavelet filtering (interquartile range = 1.5) in Homer 3 (v1.31.2; Massachusetts General Hospital, Boston, MA, USA). The motion-corrected data were visually inspected to ensure that the selected interquartile range value was well suited to the *f*NIRS data. A 4th-order Butterworth filter with a band pass of [0.001–0.2] Hz was applied to correct for physiological noise. The lowpass was set at 0.2 Hz to preserve the stimulation protocol frequency (1 / [task + mean rest] = 0.01 Hz) and the 2nd and 3rd harmonics without attenuation. HbO_2 and HHb data coming from trials characterised by < 70% level of behavioural accuracy were removed from further calculations. The haemodynamic response function (HRF) was then computed as the mean HbO_2 and HHb for each experimental condition using Matlab personal code.

For each HRF, a baseline B and plateau P were defined for HbO_2 and HHb. More specifically, the mean values of the *f*NIRS signal were computed starting 5 s before the task onset and 5 s before its end for B and P, respectively. Both indices were computed upon a 5-s time window. Then, the HbO_2 and HHb variations $\Delta = B - P$ of

an HRF were computed (for similar calculations, see Derosière et al., 2014; Mandrick et al., 2013). Finally, the mean variations $\bar{\Delta}_{HbO_2}$ and $\bar{\Delta}_{HHb}$ were given for each regions of interest (i.e., orbitofrontal, dorsolateral prefrontal, primary motor cortices).

6.2.4 *Statistical Analyses*

Because HbO_2 benefits from a better signal-to-noise ratio (see Gervain et al., 2011), only $\bar{\Delta}_{HbO_2}$ was used to support or refute hypotheses. Nonetheless, $\bar{\Delta}_{HHb}$ was also analysed and the findings are reported in Appendix B. The *f*NIRS dependent variable $\bar{\Delta}_{HbO_2}$ was analysed independently for each region of interest since the HRF was found to differ among brain regions (see Kamran et al., 2015). IRI_{error} were analysed only for the participants and trials with eligible *f*NIRS data.

To examine H_1–H_4, a twoway RM ANOVA (Motor Tempo [300, 600, 1200 ms] × Task [drawing, walking]) was applied to $\bar{\Delta}_{HbO_2}$. A similar RM ANOVA was employed to analyse the timing accuracy (i.e., IRI_{error}). Normality was checked using visual inspection of the quantile–quantile plots and the Shapiro–Wilk test. Where Mauchly's tests indicated violations of the sphericity assumption, Greenhouse–Geisser corrections were applied. Paired *t* tests with Bonferroni adjustements were used as post hoc tests where necessary. RStudio (v.1.2.5019) was used for the statistical analyses, with alpha set at $p < .05$.

6.3 RESULTS

6.3.1 *fNIRS Headset Shift*

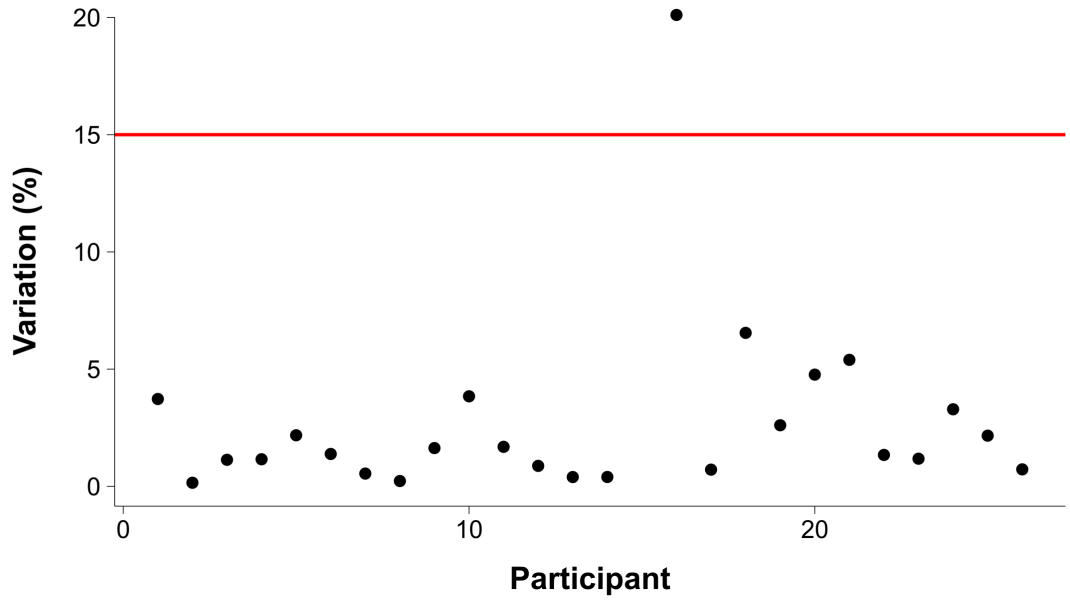
An *f*NIRS headset shift was detected for one participant (see Figure 26). Data from this participant were removed prior to further analyses. For the remaining 24 participants, the average variation of the *f*NIRS headset positioning was 2.00% (SD = 1.74).

6.3.2 *Behavioural Data*

The RM ANOVA showed a significant main effect of motor tempo, $F(2, 22) = 6.93$, $p = .005$, $\eta_p^2 = .39$, with more IRI_{error} in the 300 ms ISI ($M = 17.14$, $SD = 7.88$) than in the 600 ($p = .013$, $M = 13.45$, $SD = 5.93$) and 1200 ms ISI conditions ($p = .005$, $M = 11.92$, $SD = 3.25$). The main effect of task was also significant, $F(1, 11) = 12.09$, $p = .005$, $\eta_p^2 = .52$, with greater IRI_{error} during the drawing ($M = 16.45$, $SD = 5.64$) than during the walking task ($p < .001$, $M = 11.84$, $SD = 5.98$).

The Motor Tempo × Task interaction was significant, $F(1.35, 14.85) = 8.02$, $p = .008$, $\eta_p^2 = .42$. This indicated that IRI_{error} was greater in the 300 vs. 600 ms ($p = .033$), 300 vs. 1200 ms ($p < .001$), and 600 vs. 1200 ISI conditions ($p = .014$) during the drawing task but not during the walking task. Overall, the results indicated that participants made more timing errors in the fast externally-paced tempo condition in the drawing task only (see Figure 27).

Figure 26
fNIRS Headset Shift



Note. Variation of the *f*NIRS-head positioning for each experimental condition and participant. The red line indicates the *f*NIRS headset shift threshold at which a given participant's data were removed prior to further analyses. Data from all participants included in the study are displayed.

6.3.3 *fNIRS Data*

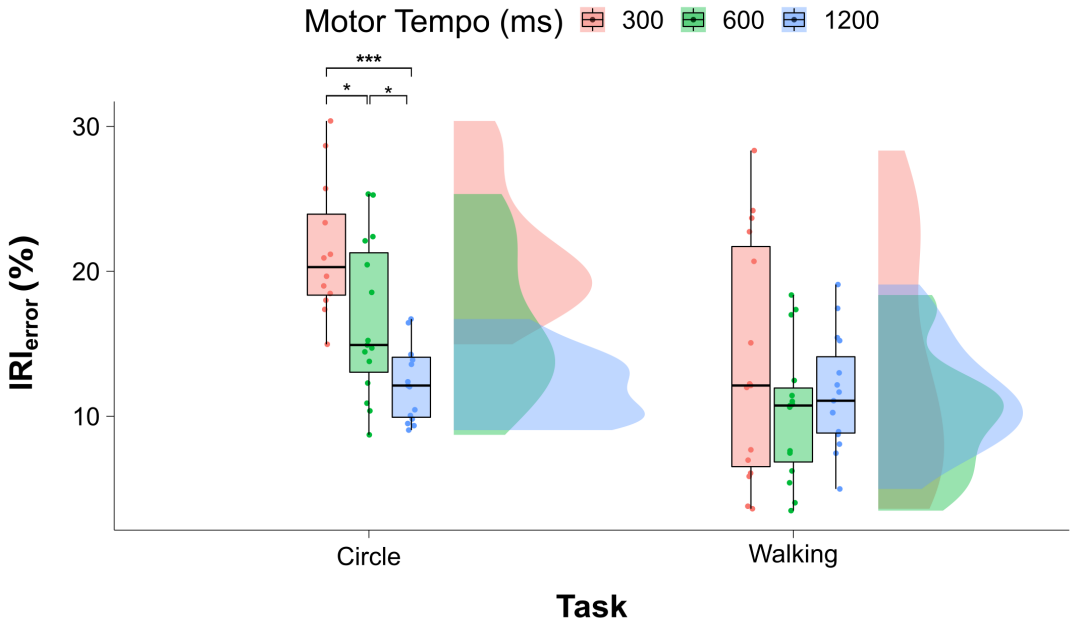
6.3.3.1 *Orbitofrontal Cortex*

The RM ANOVA did not show a significant main effect of task, $F(1, 11) = 2.28$, $p = .159$, $\eta_p^2 = .17$, or motor tempo, $F(1.26, 13.91) = 2.84$, $p = .108$, $\eta_p^2 = .20$. The Task × Motor Tempo interaction was significant, $F(2, 22) = 5.78$, $p = .010$, $\eta_p^2 = .34$, indicating that orbitofrontal cortex oxygenation was greater in the 1200 ($M = 2.09 \times 10^{-5}$; $SD = 1.50 \times 10^{-4}$) vs. 300 ISI conditions ($M = -1.19 \times 10^{-4}$; $SD = 1.61 \times 10^{-4}$; $p = .012$, Cohen's $d = 0.98$) only during the walking task (see Figure 28). Note that the effect size was larger than the required SESOI, indicating that the effect was sufficiently strong to yield meaningful results.

6.3.3.2 *Dorsolateral Prefrontal Cortex*

The RM ANOVA did not show a significant main effect of task, $F(1, 11) = 1.16$, $p = .305$, $\eta_p^2 = .09$, or motor tempo, $F(1.28, 14.04) = 0.85$, $p = .400$, $\eta_p^2 = .07$. The Task × Motor Tempo interaction was significant, $F(2, 22) = 4.14$, $p = .030$, $\eta_p^2 = .27$, indicating that the oxygenation of the dorsolateral prefrontal cortex was greater in the 1200 ($M = 1.03 \times 10^{-4}$; $SD = 1.18 \times 10^{-4}$) vs. 300 ISI conditions ($M = -7.1 \times 10^{-6}$; $SD = 1.19 \times 10^{-4}$; $p = .002$, Cohen's $d = 1.22$) only during the walking task (see Figure 28).

Figure 27
Timing Accuracy for Each Experimental Condition



Note. Box plots and density distributions are displayed for each designated motor tempo and task. Each dot represents an individual participant. * $p < .050$, *** $p < .001$.

Note that the effect size was larger than the required SESOI, indicating that the effect was sufficiently strong to yield meaningful results.

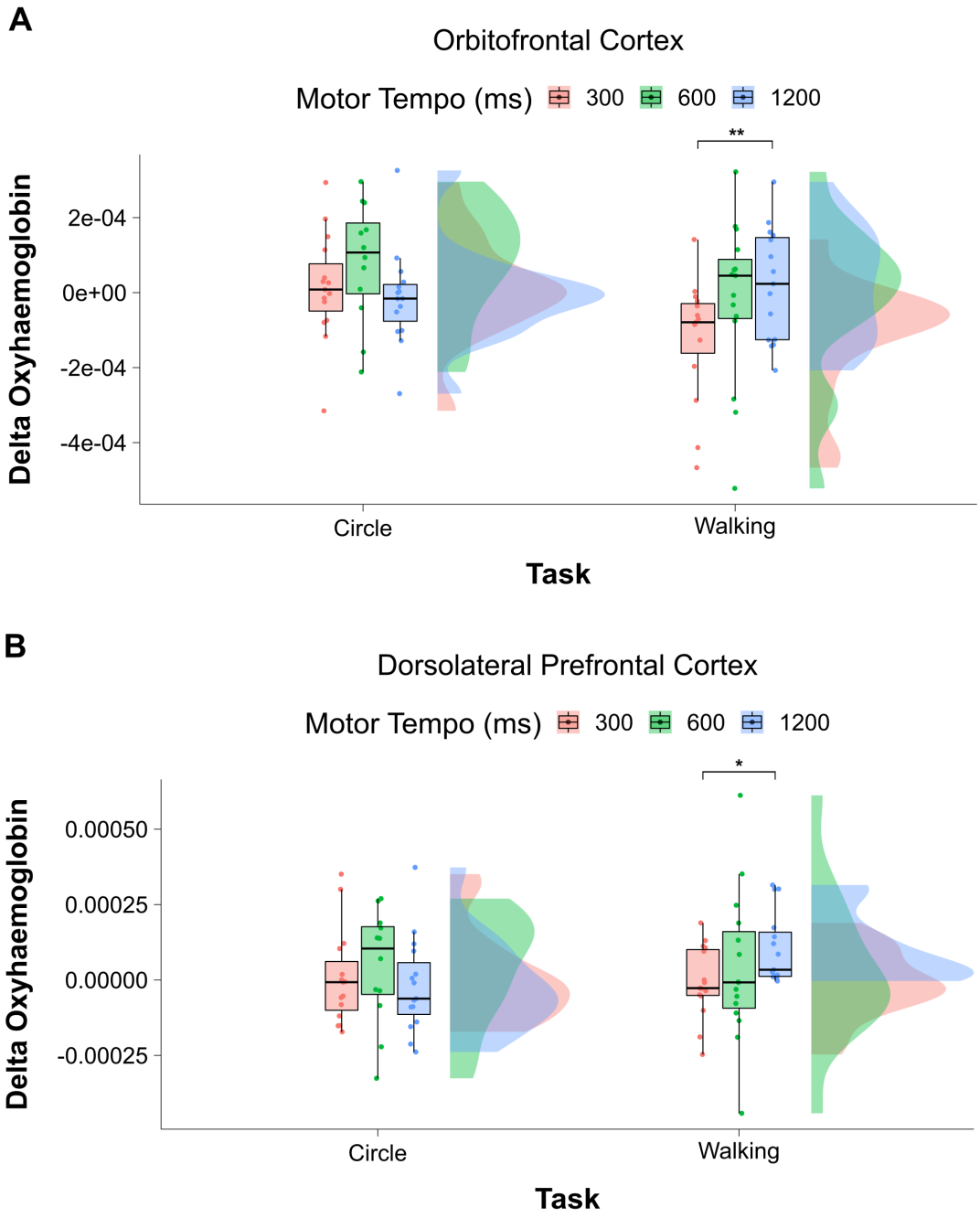
6.3.3.3 *Premotor Cortex and SMA*

The RM ANOVA showed a significant main effect of task, $F(1, 11) = 7.55$, $p = .019$, $\eta_p^2 = .41$, with higher premotor cortex and supplementary motor area oxygenation in the walking ($M = 1.58 \times 10^{-4}$, $SD = 1.85 \times 10^{-4}$) than in the circle drawing task ($M = 4.43 \times 10^{-5}$, $SD = 1.87 \times 10^{-4}$, Cohen's $d = 0.48$; see Figure 29). The main effect of motor tempo was non significant, $F(1.26, 13.9) = 0.66$, $p = .464$, $\eta_p^2 = .06$. The Task $\times$ Motor Tempo interaction was non significant, $F(2, 22) = 1.96$, $p = .164$, $\eta_p^2 = .15$.

6.3.3.4 *Primary Motor Cortex*

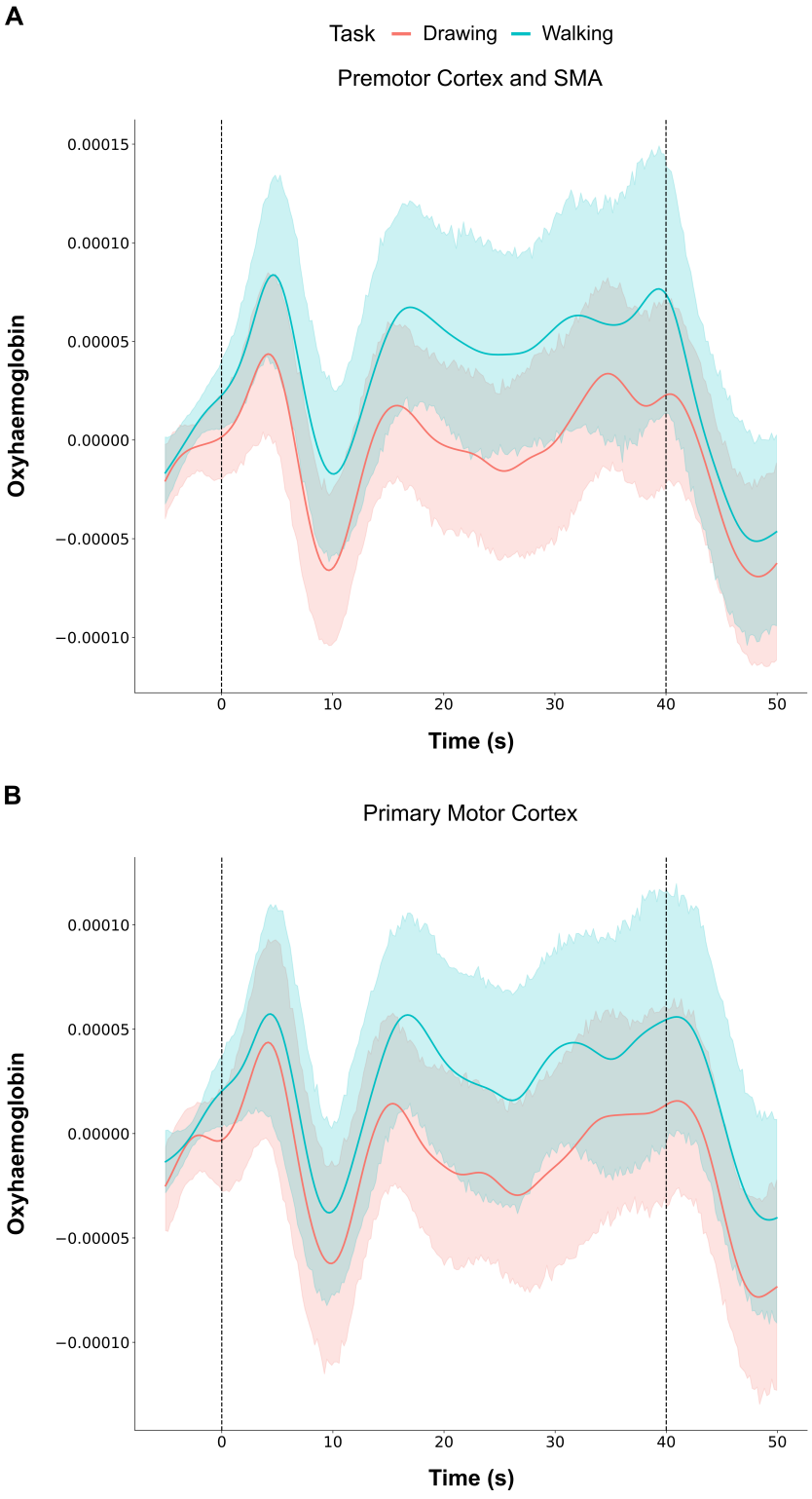
The RM ANOVA showed a significant main effect of task, $F(1, 11) = 9.80$, $p = .010$, $\eta_p^2 = .47$, with greater primary motor cortex oxygenation during the walking ($M = 2.11 \times 10^{-4}$, $SD = 2.25 \times 10^{-4}$) than during the drawing task ($M = 6.40 \times 10^{-5}$, $SD = 2.32 \times 10^{-4}$, Cohen's $d = 0.51$; see Figure 29). The main effect of motor tempo was non significant, $F(2, 22) = 0.65$, $p = .533$, $\eta_p^2 = .06$. The Task $\times$ Motor Tempo interaction was non significant, $F(1.36, 14.96) = 1.73$, $p = .212$, $\eta_p^2 = .14$. Note that the effect size was larger than the required SESOI, indicating that the effect was sufficiently strong to yield meaningful results.

Figure 28
fNIRS Results for the Prefrontal Cortex



Note. Box plots and density distributions are displayed for each designated motor tempo and task. Each dot represents an individual participant. * $p < .050$, ** $p < .010$.

Figure 29
fNIRS Results for the Motor Cortex



Note. Mean oxyhaemoglobin data for each designated task. 95% confidence intervals are represented by the shaded area that surrounds each trace. SMA = supplementary motor area.

6.3.4 *Exploratory analyses*

6.3.4.1 *Lateralisation of Prefrontal Activations*

To examine the respective contributions of the two cerebral hemispheres, additional RM ANOVAs were computed on $\bar{\Delta}_{HbO_2}$ over the prefrontal regions for the left and right hemispheres, separately. In the orbitofrontal cortex, the RM ANOVAs were significant for both the left, $F(2, 22) = 7.88$, $p = .003$, $\eta_p^2 = .42$, and right hemispheres, $F(2, 22) = 3.53$, $p = .047$, $\eta_p^2 = .24$. Post hoc tests indicated that the orbitofrontal cortex oxygenation was greater in the 1200 vs. 300 ms ISI conditions only during the walking task ($p_{left} = .005$, $d_{left} = 1.08$, $p_{right} = .006$, $d_{right} = 1.08$).

In the dorsolateral prefrontal cortex, only the RM ANOVA conducted on the left hemisphere was significant, $F(2, 22) = 6.20$, $p = .007$, $\eta_p^2 = .36$. Post hoc tests indicated that the left-dorsolateral cortex oxygenation was greater in the 1200 vs. 300 ms ISI conditions only during the walking task ($p = .012$, $d = 1.00$). The RM ANOVA conducted on the right hemisphere was non significant, $F(2, 22) = 1.84$, $p = .183$, $\eta_p^2 = .143$.

6.3.4.2 *Correlations*

To investigate the possible relation between behavioural performance and cerebral oxygenation, the linear correlation between the IRI_{error} and prefrontal activation in the slow walking trials was computed. Pearson's correlation coefficient was used ($\alpha = .05$) and the normality of the distributions was checked through visual inspection of the quantile–quantile plots. The correlation was non significant for the bilateral orbitofrontal ($r = .27$, $t(13) = 1.02$, $p = .163$) and left dorsolateral prefrontal cortex ($r = .21$, $t(13) = .77$, $p = .227$).

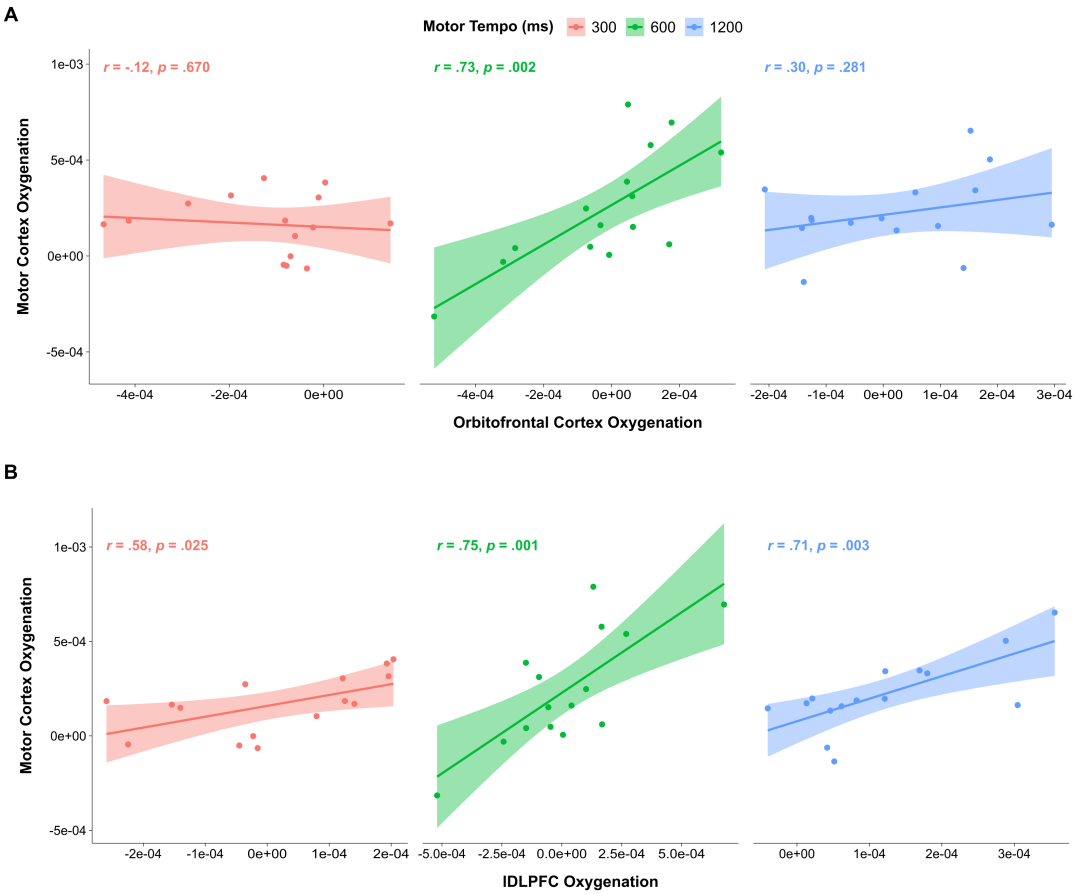
Additional Pearson's correlation coefficients were computed to further examine the connection between the prefrontal and the motor regions as a function of motor tempo during the walking task. The correlation between the bilateral orbitofrontal and primary motor cortices oxygenation was significant in the close-to-spontaneous paces ($r = .73$, $t(13) = 3.82$, $p = .002$), but not in the slow ($r = .30$, $t(13) = 1.13$, $p = .281$) and fast paces ($r = -.12$, $t(13) = -0.43$, $p = .670$; see Figure 30). In addition, the correlation between the oxygenation levels of the left dorsolateral prefrontal and bilateral primary motor cortices was significant in the slow ($r = .71$, $t(13) = 3.64$, $p = .003$), close-to-spontaneous ($r = .75$, $t(13) = 4.06$, $p = .001$), and fast paces ($r = .58$, $t(13) = 2.54$, $p = .025$; see Figure 30).

6.3.4.3 *Beginning vs. End of Trials*

To examine the cerebral oxygenation dynamics over the course of a trial, additional twoway RM ANOVAs (Motor Tempo [300, 600, 1200 ms] $\times$ Period [beginning, end]) were applied to $\bar{\Delta}_{HbO_2}$ for each task separately. The value for the end of a trial was computed as the mean $\bar{\Delta}_{HbO_2}$ value over the last 5 s, as previously computed. The value for the beginning of a trial was calculated as the mean $\bar{\Delta}_{HbO_2}$ over the first

Figure 30

Correlation Between Prefrontal and Motor Oxygenation



Note. Linear regression lines and associated 95% confidence intervals are displayed for each designated motor tempo. lDLPFC = left dorsolateral prefrontal cortex.

10–15 s[1]. In the interest of conciseness, only the significant main effect and interaction of period are reported.

PREFRONTAL CORTEX. For the drawing task, the RM ANOVAs showed a significant Motor Tempo × Period interaction in the bilateral orbitofrontal, $F(2, 22) = 4.89$, $p = .017$, $\eta_p^2 = .31$, and left dorsolateral prefrontal cortices, $F(2, 22) = 3.58$, $p = .045$, $\eta_p^2 = .27$. Nonetheless, the post hoc tests were non significant. For the steady-state walking task, the RM ANOVAs did not show any significant effects of period.

MOTOR CORTEX. For the drawing task, the RM ANOVAs showed a significant Motor Tempo × Period interaction in the primary motor cortex, $F(2, 22) = 4.14$, $p = .030$, $\eta_p^2 = .27$, and premotor cortex and supplementary motor area, $F(2, 22) = 4.90$,

1 This time range was chosen because it coincides with the beginning of the canonical haemodynamic response.

p = .017, η_p^2 = .31. Nonetheless, the post hoc tests were non significant for the two regions of interest.

For the steady-state walking task, the RM ANOVA showed a significant main effect of period in the primary motor cortex, $F(1, 14) = 8.43$, p = .012, η_p^2 = .38, and premotor cortex and supplementary motor areas, $F(1, 14) = 5.48$, p = .035, η_p^2 = .28 This indicated higher cerebral oxygenation for the end vs. beginning ($d_{\text{premotor}} = 0.48$, $d_{\text{motor}} = 0.56$) of trials across the motor areas.

6.4 DISCUSSION

The main purpose of the present study was to investigate prefrontal and motor brain activity during the execution of voluntary continuous movements at various tempi. Two motor tasks (i.e., drawing and steady-state walking) were employed in a SMS paradigm performed at fast (i.e., 300 ms), natural (i.e., 600 ms), and slow paces (i.e., 1200 ms). The walking task led to greater motor oxygenation than the circle-drawing task. Accordingly, H_1 was verified. Action production at slow pace yielded more prefrontal activation when compared to action production at close-to-spontaneous and faster paces but this pattern was observed during the walking task only. Thus, H_2 was only partially confirmed and H_3 was verified. Finally, the slow tempi trials did not lead to less motor activity when compared the close-to-spontaneous and fast tempi trials. Hence, H_4 was not confirmed.

6.4.1 *Type of Motor Behaviours*

The first major result reported here was the fact that both types of motor tasks did not yield similar behavioural and cerebral outcomes. Non-automatic movements (i.e., drawing) led to higher timing errors and were more affected by motor tempo than automatic movements (i.e., walking), which replicate our previous results (Rose et al., 2021). These findings resonate with the notion that walking is a phylogenetically old motor activity that is completely automatic (Schaal et al., 2004). Modulating the pace of such usual patterns of body movements is relatively easy, which is not the case for less ingrained actions.

The larger timing errors observed in the drawing task were not associated with increased prefrontal activity. Thus, it may be presumed that performing and modulating the pace of upper-limb movements did not require additional cognitive resources. An alternative hypothesis is that whole-body motor behaviours benefited from higher entrainment (i.e., temporal locking process in which a signal frequency entrains the frequency of a system; Thaut, 2013). The entrainment process has indeed been shown to optimise motor planning and execution, possibly through spontaneous adjustments of neural dynamics (Nozaradan et al., 2011; Thaut et al., 2015). This notion is corroborated in the present study by the findings that greater motor oxygenation was observed during the execution of the walking when compared to the drawing task.

6.4.2 *Cerebral Oxygenation Dynamics*

An original contribution of the present study concerns the investigation of the haemodynamic response dynamics. The primary motor cortex oxygenation was found to increase from the beginning to the end of the walking trials. These results are consistent with the findings reported in sport sciences and confirm that gradual increases in oxyhaemoglobin level are observed during the execution of a motor task (e.g., Fumoto et al., 2010). Such cerebral phenomenon can be attributed to the filling of nutritional requirements in the motor regions of the brain. Notably, the progressive increased in nutritional requirements would be induced by the sustained activity of the motor neurons supporting muscular activity. This would explain the absence of a gradual rise in motor activity during the time course of the circle trials, which did not require a lot of muscular effort.

In the present study, the length of the experimental trials (i.e., 40 s) enabled the researchers to contrast the cerebral oxygenation at the beginning vs. end of the motor task execution. Nonetheless, most of the studies using motor paradigms employed shorter trials (~15 s; e.g., Batula et al., 2017; Caçola et al., 2018; Curzel et al., 2021) that do not permit the investigation of haemodynamic activity over time. Thus, future researchers need to carefully consider the length of trial that is most suitable in addressing their research hypotheses. Lengthy trials (e.g., > 30 s) might be useful to examine subtle variations in the pattern of cerebral activation observed in the course of a cognitive process.

6.4.3 *Dorsolateral Prefrontal Cortex Supports the Production of Synchronised Movements*

It is notable that the prefrontal cortex (i.e., orbitofrontal and dorsolateral regions) was activated to a greater extent during the production of slow vs. fast movements. Specifically, this effect was observed only during the whole-body walking task. Supplementary analyses showed that only the left part of the dorsolateral cortex was activated during the slow walking trials. It is the case that the dorsolateral prefrontal cortex plays a critical role in inhibition, planning, and working memory (Curtis & D'Esposito, 2003; Oldrati et al., 2016; Tanji & Hoshi, 2001). Nevertheless, the right and left part of these areas have been reported to provide specific functional contributions. More precisely, the right dorsolateral prefrontal cortex was shown to be related to sustained attention and learning processes (Mannarelli et al., 2015; Tomasino & Fabbro, 2016). The right dorsolateral prefrontal cortex was also found to be involved in time production especially in tasks for which decisions regarding the timing of movements were to be made (Jenkins et al., 2000). Nonetheless, the findings of the present study provide first evidence suggesting that the right dorsolateral prefrontal cortex does not play a sensitive role in the pacing of movement.

Activity in the left part of the dorsolateral prefrontal cortex has been related to inhibition of response *planning* rather than response *execution* (Kadota et al., 2010). Therefore, the left dorsolateral prefrontal cortex could support movement planning instead of motor inhibition per se. Notably, the left dorsolateral cortex has been also reported to be involved in goal prioritisation and decision making (Kaller et al., 2011; Turnbull et al., 2019). For example, Heekeren et al. (2006) proposed that the

left part of the dorsolateral prefrontal cortex acts as a "comparator" by integrating information from the motor and sensory areas to make decisions and guide subsequent behaviours. This notion is corroborated by the positive correlations found in the present study between activation in the left dorsolateral prefrontal cortex and the primary motor cortex, regardless of motor pace.

When producing a movement at a slow pace, the integration of multidimensional information has time to be implemented, which is not the case when moving at fast tempi (see Guérin et al., 2021a). This could provide a plausible explanation for the enhanced left dorsolateral prefrontal activity observed in the present study during the slow walking trials. Consequently, we propose that the dorsolateral prefrontal cortex may be involved in the production of timed behaviours, but not necessarily in decreasing the pace of spontaneous movements. Future research would need to compare the involvement of the dorsolateral prefrontal cortex in synchronisation vs. self-paced movements.

6.4.4 *Motor Inhibition is Underpinned by Orbitofrontal Activation*

In a previous study using *f*MRI, the orbitofrontal cortex was found to be active when participants performed a cognitive task requiring inhibition (Horn et al., 2003; Rubia et al., 2001). In addition, patients with focal lesions to the medial orbitofrontal cortex were significantly impaired during the inhibition of irrelevant responses (Szatkowska et al., 2007). Thus, the greater orbitofrontal activation found in the present study during slow walking trials suggest that inhibition is needed to produce movements slower than the spontaneous pace. More specifically, inhibitory control would be a key process in restraining the urge to move at spontaneous pace. As scientific knowledge stands, the neurobiological origin of the spontaneous motor tempo is still unknown to the scientific community (Morillon et al., 2019). Nonetheless, it could be that prefrontal inhibitory signals are sent to the motor neurons in order to decelerate the speed of neural trajectories in the motor regions (see Buonomano & Karmarkar, 2002).

The fact that this prefrontal phenomenon was found only during the walking task suggests that inhibitory control is particularly salient for locomotor behaviours. It has been shown that the temporal structure for a given movement is not transferable to another movement (Buonomano & Karmarkar, 2002). It is arguable that the walking behaviour is so natural and habitually performed that its neural trajectories are characterised by stronger synaptic weights when compared to less stereotyped behaviours. Thus, a larger degree of inhibitory control would be needed to decelerate the speed of the neural trajectories coding for locomotion.

Results of the present study showed that performing a task at slow pace did not induce less activity in the motor areas of the brain when compared to performing the same task at fast pace. This pattern of results is in contradiction with our previous results (Guérin et al., 2021c). Explanation for this unexpected finding might lies with the nature of the motor tasks that were used. Guérin et al. (2021c) employed only upper-limb movements (i.e., finger tapping and circle drawing) that entailed different cognitive processes from those engaged during whole-body motor behaviours. Another plausible hypothesis is that the production of fast and slow movements are

not underlined by two distinct processes, as suggested in the scientific literature (e.g., Lewis & Miall, 2003a; Wiener et al., 2010a). Rather, we advocate the existence of a single motor processing mechanism for the production of fast and slow movements; an additional cognitive process – the most likely candidate being motor inhibition – would be required for the production of body movements slower than the spontaneous natural tempo.

6.4.5 *Limitations and Future Directions*

A limitation pertaining to the experimental paradigm used is that participants had to synchronise their motor responses with an auditory stimulus (i.e., beep). Such SMS might have entailed distinct motor-timing processes than those engaged during self-paced actions. The left dorsolateral activation reported in the present study could be attributed to a by-product of the synchronisation process rather than to the effect of motor tempo per se. More research is needed to provide a fuller picture of the prefrontal pattern of activity involved in motor timing and dissociate the specific contributions of the dorsolateral prefrontal and orbitofrontal cortices.

A second limitation lies with the apparent variability of our *f*NIRS signals (see Figure 29). Even if three trials are commonly used in *f*NIRS studies employing a block-design procedure (Menant et al., 2020), more trials might have been beneficial to reduce the variability of individual mean haemodynamic responses.

6.4.6 *Conclusions*

The present chapter makes an original theoretical contribution by advocating that the production of slow movements relies on the same brain processes than those needed for the production of fast movements. Slow movements would, in addition, need cognitive monitoring in order to ensure slow pacing of movements. The orbitofrontal cortex would be a suitable candidate for slow-paced movements, especially when targeting phylogenetically old behaviours such as walking.

INTERMEDIATE SUMMARY

Human beings are skilled when it comes to adapt the pace of their movements to environmental constraints. While the production of fast movements would rely on motor processes, the ability to slow down the pace of motor behaviours may be underpinned by cognitive control (i.e., motor inhibition). Yet, the brain correlates of temporal motor control is still largely unknown. The general aim of Chapter 6 was to examine prefrontal and motor activity during the execution of motor tasks (i.e., drawing and walking) performed under different time constraints. Brain activity was recorded using *f*NIRS over the bilateral primary motor and prefrontal cortices (i.e., orbitofrontal and dorsolateral regions) because of their involvement in inhibitory control. The two motor tasks were implemented in a SMS paradigm with trials performed at fast (i.e., 300 ms), close-to-spontaneous (i.e., 600 ms), and slow paces (i.e., 1200 ms).

Results showed that the walking task led to greater bilateral SMA and primary motor cortex oxygenation than the circle-drawing task. Action production at slow pace yielded more bilateral orbitofrontal and left dorsolateral activation when compared to action production at close-to-spontaneous and faster paces; this pattern was observed in the walking task only. These findings support the key role of prefrontal cognitive control in the production of slow movements. In addition, the brain mechanisms for inhibiting spontaneous motor pacing are particularly salient in phylogenetically old movements such as walking. Nonetheless, additional studies employing a wide range of action classes are required to further confirm this hypothesis.

Chapter 6 has been submitted for publication and is currently under review. In addition, the results were the subject of two conference presentations (2021, 19ème Congrès de l'Association des Chercheurs en Activités Physiques et Sportives, Montpellier, France; *f*NIRS 2021, Boston, USA).

*f*NIRS brain imaging provides the research with the means to record cerebral activity of moving individuals. Nonetheless, there is a dearth of evidence-based recommendations to guide experimental protocol building and data acquisition. The general aim of Chapter 7 was to address this methodological ellipsis by investigating the number of required trials for block-design procedure, test–retest reliability and headset stability in *f*NIRS brain imaging during motor paradigms.

7

METHODOLOGICAL INVESTIGATIONS IN *f*NIRS BRAIN IMAGING

7.1 INTRODUCTION

Functional imaging provides insight into the brain processes involved in human behaviours. Over the last century, several functional neuroimaging techniques (e.g., *f*MRI, EEG, magnetoencephalography, positron emission tomography) were developed to highlight the anatomical arrangements and temporal dynamics of the nerve cells engaged in human conducts. These various neuroimaging modalities enabled the scientific community to investigate the brain processes involved in various cognitive tasks (e.g., visual perception, recollection, language processing; see Dehaene-Lambertz et al., 2006; Eden et al., 1996; Ungerleider, 1995). Nonetheless, recording brain activity during motor paradigms still represents a major challenge for neuroscientists. Motor artefacts jeopardise brain signals and current neuroimaging modalities suffer from severe restrictions in terms of movement (Herold et al., 2018).

*f*NIRS is a neuroimaging technique that was introduced in 1993, and which has seen exponential growth in its usage in the intervening three decades (Yücel et al., 2017). *f*NIRS has several advantages over other imaging modalities that include low acquisition costs, continuous long-time monitoring, short installation time, portability, and robustness to motion artefacts (Leff et al., 2011). Making use of infrared light, the non-invasive *f*NIRS technology monitors the relative changes in HbO_2 and HHb concentrations within the cerebral cortex, facilitating a recording depth of ~0.5–2.0 cm (Huppert, 2016).

The so-called *neurovascular coupling* phenomenon refers to a close relationship between local neural activity and changes in cerebral blood flow. Because there are no reserves of energy fuels available to the brain, neuronal activity engenders local energy requirements. The brain has the ability to rapidly increase the cerebral blood flow to deliver oxygen and nutrients (e.g., glucose) to the active neurons via the astrocytes (MacVicar & Newman, 2015). This leads to an increase in HbO_2 and a decrease in HHb concentrations that can be used to infer cortical activation levels.

The *f*NIRS technique has been successfully used to monitor brain activation during single-limb movements (e.g., Batula et al., 2017; Leff et al., 2011; Rahimpour et al., 2020) and more complex motor tasks (e.g., Huang et al., 2019; Seidel et al., 2019; Tempest & Reiss, 2019). In addition, *f*NIRS is a promising tool in the investigation of cortical activity elicited by natural behaviours in ecological settings (see Curtin & Ayaz, 2018; Pinti et al., 2020). Nonetheless, reproducibility of *f*NIRS results – in particular at the within-subject level – as well as comparison across studies remain challenging (see Blasi et al., 2014; Plichta et al., 2006; Yücel et al., 2021; Zhang et al., 2011). This is mainly due to the considerable variability existing in the experimental designs and analytical techniques used (Hocke et al., 2018; Luke et al., 2020; Pinti

et al., 2019), and the lack of spatial information regarding the positioning of *f*NIRS optodes (Novi et al., 2020).

A huge limitation of the *f*NIRS technique is the dearth of evidence-based recommendations to guide experimental protocol building. Surprisingly, the number of trials required to obtain a robust haemodynamic response remains unknown (Herold et al., 2017). A rule of thumb is to use at least three trials to perform averaging over several *f*NIRS signals (i.e., block design; Menant et al., 2020). Yet, this may seem a negligible amount when compared to the 50–100 trials required in EEG studies to reduce the variability of the recorded brain signals (see Boudewyn et al., 2018; Mouraux & Iannetti, 2008). Averaging an insufficient number of trials can lead to an erroneous pattern of brain response and misinterpretation of the data, which could explain the lack of reproducibility in the field of *f*NIRS (Novi et al., 2020).

When conducting experimental investigations using motor paradigms, a major consideration is the position of the headset holding the *f*NIRS optodes with regard to the participant's head. In *f*NIRS experiments, a common strategy is to use the international 10–20 system to place the optodes (i.e., source–detector array) over the cerebral regions of interest (Herold et al., 2018). However, the execution of a motor task can lead to a shift in the *f*NIRS headset position. When such a shift occurs, it is impossible to know with precision the anatomical locations of the recorded haemodynamic signals.

The first aim of the present study was to define the appropriate number of trials necessary to obtain a robust haemodynamic response using *f*NIRS. The second aim was to perform test–retest reliability of the *f*NIRS results over several days at the within-subject level. Finally, the third aim was to report a procedure that was develop to ensure the stability of the *f*NIRS headset over an experimental session during whole-body movement tasks.

7.2 METHODS

7.2.1 *Participants*

Three female participants were recruited for the present study from among the corpus of University of Lille staff. Participants provided written informed consent. Participants had a normal vision, and did not present motor dysfunction or neurological/psychiatric disorders. The characteristics of the three participant are provided in Table 9. The ethics committee of the University of Lille (France) approved the study (see Appendix A).

7.2.2 *Materials and Data Acquisition*

A FOIRE-3000/16 *f*NIRS system (Shimadzu, Kyoto, Japan) was used to record participants' cerebral-haemodynamic activity while they performed a motor task. This continuous-wave system uses optical fibers with wavelenghts of 780, 805, and 830 nm. The sampling rate was set at 4.55 Hz (i.e., 220 ms). The fOLD toolbox (Morais et al., 2018) was used to ascertain the channel arrangement needed to record haemodynamic activity from the bilateral primary motor cortex. A 20-channel model con-

Table 9
Demographic Characteristics of the Participants

Participant	Age	Handiness	Head measurements		Hair Characteristics
			Pre-auricular distance	Nasion–inion distance	
1	25	Left-handed	37.5	41.6	Brown, long, standard thickness
2	29	Right-handed	34.5	38.5	Light brown, long, fine
3	19	Left-handed	37.5	40	Dark brown, long, thick

Note. Head measurements are provided in centimetres.

sisting of eight sources and ten detectors was used, with the interoptode distance set to 3 cm. The headset was placed on each participant's head in accord with the International 10–20 system guidelines for standard electrode positions (Jasper, 1958).

Three motor tasks were used in the present study: finger tapping, recumbent cycle ergometry, and upright cycle ergometry. The finger-tapping task was performed via a touchscreen (1915L Elo Touch 19"; Elo TouchSolutions Inc.; Milpitas, California, CA) placed on a table in front of the participant. The screen was oriented at 45° to facilitate the participant's movements. The participant was seated on a non-rotational stool to avert any superfluous movements during the task execution.

Two cycling tasks were performed (i.e., upright and recumbent cycle ergometry) to examine the impact of upper-body stability (see Figure 31). A Domyos E Seat ergocycle (Decathlon, Villeneuve d'Ascq, France) and Monark Ergomedic 874E ergocycle (Vansbro, Sweden) were used for the recumbent cycling task and the upright cycling task, respectively. The flywheel resistance was set at minimum value (i.e., 1 kg for the Monark ergocycle and 20 W for the Domyos ergocycle).

A MP150 Biopac system (Biopac Systems, Goleta, CA) was used to monitor heart and respiration rates. Heart-rate data was recorded using a BN-EL30-LEAD3 lead set, with two EL503 disposable-patch electrodes positioned on the participant's right and left clavicles. Respiration-rate data were captured via a BN-RESP-XDCR transducer,

Figure 31
Equipment Used in the Three Experimental Tasks

Note. Left panel: Tactile screen. Middle panel: Recumbent cycle ergometry. Right panel: Upright cycle ergometry.

placed around the thoracic region below the sternum. Both Biopac devices were attached to a Dual Wireless Respiration and ECG BioNomadix transmitter, connected to a RPEC-R amplifier. Sampling frequency was set to 250 Hz. Data acquisition was managed through the Acq*Knowledge* software that is included in the MP system.

Motion-capture data were collected using six Oqus 5+ cameras (Qualisys Mo-Cap, Göteborg, Sweden) and five spherical passive markers. Three cameras were directed towards the participant's head to track the *f*NIRS headset position (one marker on the participant's temple and two on the headset). During the two cycling tasks, three others cameras were also oriented towards the participant's feet to monitor behavioural performance (two markers on the feet). Sampling frequency was set to 50 Hz, and the spatial accuracy of the system (i.e., residuals) was < 0.2 mm for each dimension of the 3D space.

7.2.3 *Experimental Procedure*

7.2.3.1 *Tasks Description*

Each participant completed three experimental tasks. In the finger-tapping task, the participant was required to tap with their dominant-hand index finger on a visual target (black dot of 10-mm diameter; see Figure 31) placed in the center of the touchscreen. In the two cycling tasks, the participant was asked to pedal while keeping their hands on the ergocycle handles. In each of the aforementioned tasks, the participant was instructed to synchronise their movements to the pace of a regular metronome (ISI = 600 ms, duration = 80 ms, sound frequency = 294 Hz.). The participant was asked not to speak and to avoid any extraneous movements during the recordings.

7.2.3.2 *Experimental Design*

During the experimental session, the participant performed one of the three tasks (i.e., finger tapping, recumbent cycling, and upright cycling). The participant completed each task three time on a different day. Thus, each participant made nine visits to the laboratory over the course of 5 weeks. An experimental session consisted in 50 trials. Each 40-s trial was preceded by a baseline period between 25–35 s. An experimental session lasted for ~90 min.

7.2.4 *Preprocessing*

7.2.4.1 *Behavioural Data*

Behavioural accuracy was assess by calculating (a) the time interval between the onset of successive taps for the finger-tapping task and (b) the time interval between to pedal strokes for the cycling tasks. Specifically, the IRI_{error} was computed as the percentage of absolute difference between an IRI and the reference ISI for a given time interval t (see Equation 4). IRIs were extracted from the touchscreen data for the finger-tapping task, and from the motion-capture data for the cycling tasks (see Section 6.2.3.1 for similar calculations).

7.2.4.2 *fNIRS-Headset Shift Data*

The mesh area (i.e., the deformation calculation of the triangular area connecting the three 3D markers) was computed to verify the stability of the *f*NIRS headset in relation to the head. If relative position of the 3D markers remained consistent, the mesh area should remain constant. On the other hand, if the two headset markers moved relatively to the temple marker, the mesh area would be modified accordingly.

The mesh area between the three markers was computed on a 15-s window using a scalar product (see Equation 1), equal to twice the mesh area. The variation of the $\overrightarrow{M_0M_1} \cdot \overrightarrow{M_0M_2}$ value between the beginning (i.e., 60 s after the beginning of the file) and end (i.e., 75 s before the end of the file) of an experimental session was then computed as a percentage and referred to as $\Delta_{\text{beginning–end}}$. An *f*NIRS headset shift was detected if this value exceeded 15% (see Section 2.3.2).

To ensure that no headset shift has occurred during the experimental session, the variation in *f*NIRS positioning was also computed over the course of an entire experimental session. More precisely, $\overrightarrow{M_0M_1} \cdot \overrightarrow{M_0M_2}$ was computed on a 15-s window every 15 s. The variation among the first $\overrightarrow{M_0M_1} \cdot \overrightarrow{M_0M_2}$ value and every k subsequent value was then calculated as a percentage, referred to as Δ_k.

7.2.4.3 *fNIRS Data*

The preprocessing pipeline of *f*NIRS data was similar to that of Chapter 6. Briefly, differences in the absorption of HbO_2 and HHb were computed using Equation 5 and 6. Correction for motion artefacts was performed using wavelet filtering (interquartile range = 1.5) in Homer 3 (v1.31.2; Massachusetts General Hospital, Boston, MA, USA). The motion-corrected data were visually inspected to ensure that the selected interquartile range value was well suited to the *f*NIRS data. A 4th-order Butterworth filter with a band pass of [0.001–0.2] Hz was applied to correct for physiological noise while preserving the stimulation protocol frequency (1 / [task + mean rest] = 0.01 Hz).

The HRF was computed as the mean HbO_2 and HHb for each experimental condition using Matlab personal code. For each HRF, the variation Δ of HbO_2 and HHb were computed upon a 5-s time window (baseline = -5–0 s , plateau = 35–40 s). Data from each individual channels were eventually averaged to have a single $\bar{\Delta}_{HbO_2}$ and $\bar{\Delta}_{HHb}$ value for the primary motor cortex.

7.2.5 *Data Analyses*

Data of the present chapter are currently being analysed. Thus, only preliminary analyses are reported in the following section. For the time being, only $\bar{\Delta}_{HbO_2}$ was examined.

Visual inspection was performed to detect the number of trials needed to stabilise the haemodynamic response of the brain (i.e., elbow approach). To examine the test–retest reliability of the *f*NIRS signals, a twoway RM ANOVA (Task [recumbent cycling, upright cycling, finger tapping] $\times$ Session [1, 2, 3]) was applied to $\bar{\Delta}_{HbO_2}$ (averaged over the 50 trials). In addition, Pearson correlation coefficients of the hemodynamic-signal time course among the three sessions were computed at

the individual level (for a similar procedure, see e.g., Blasi et al., 2014; Huang et al., 2017).

7.3 PRELIMINARY RESULTS

The results detailed in this section are, for the most part, the outcomes of descriptive and visual examination of the data.

7.3.1 *Behavioural Data*

Mean IRI_{error} for each session and participant is presented in Figure 32. The results showed that participants produced overall very few errors as none of them exceed the threshold established in Chapters 4 and 6 (i.e., 30%). It is notable that Participant 2 made more IRI_{error} (M = 4.61%, SD = 1.88) than the two other participants ($M_{Participant\ 1}$ = 3.16%, $SD_{Participant\ 1}$ = 1.15; $M_{Participant\ 3}$ = 3.67%, $SD_{Participant\ 3}$ = 1.54). Participant 2 made a maximum timing error of 16% when compared to 8% for Participants 1 and 3. For each participant, the finger-tapping task seemed to elicit more timing errors than the two cycling tasks (see Figure 32).

7.3.2 *Stability of the fNIRS Headset*

An *f*NIRS headset shift was detected for Participant 1 during the third session of the recumbent-cycling task ($\Delta_{beginning–end}$ = 17.83%; see Figure 33). Excluding the aforementioned value, the average variation of the *f*NIRS headset positioning was 0.80% (SD = 0.67) for the recumbent-cycling task, 2.12% (SD = 2.37) for the upright-cycling task, and 0.73% (SD = 1.31) for the finger-tapping task.

To ensure that no headset shift had occurred during the experimental session, the variations Δ_k of the *f*NIRS-headset positioning over an entire experimental session were also examined. The maximum Δ_k values were extracted for each participant and experimental condition (see Table 10). No other *f*NIRS-headset shift was detected than that of Participant 1.

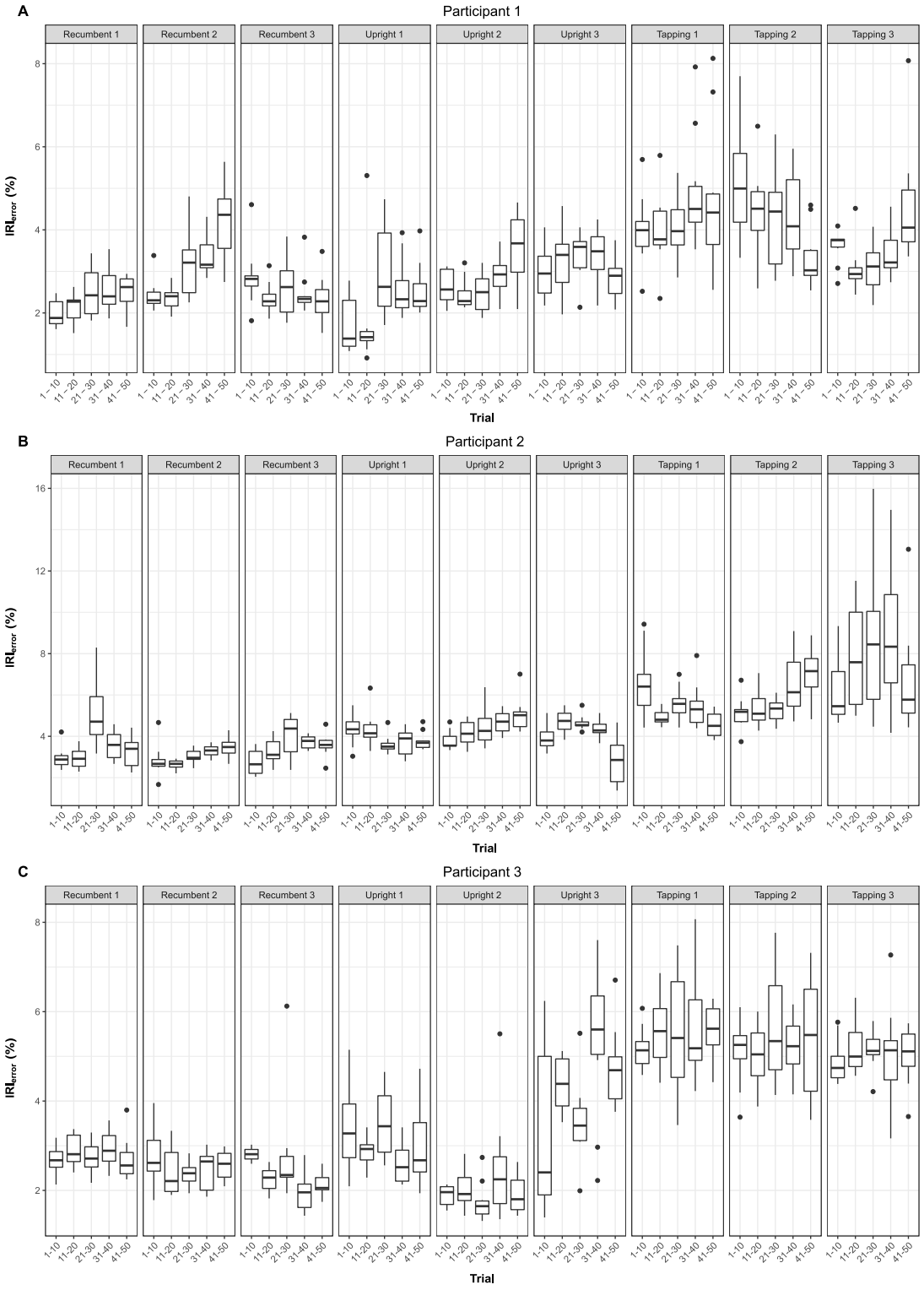
Table 10
Maximum Δ_k Value

Session	Participant 1			Participant 2			Participant 3		
	Recumbent	Upright	Tapping	Recumbent	Upright	Tapping	Recumbent	Upright	Tapping
1	0.29	0.96	3.08	0.45	1.19	1.05	0.82	2.63	1.72
2	1.32	2.23	1.36	4.67	0.56	1.09	1.18	2.67	0.71
3	18.48	8.10	1.10	1.33	6.04	1.09	0.80	1.29	1.08

Note. Data are given in percentage. Recumbent = recumbent cycling; upright = upright cycling; tapping = finger tapping.

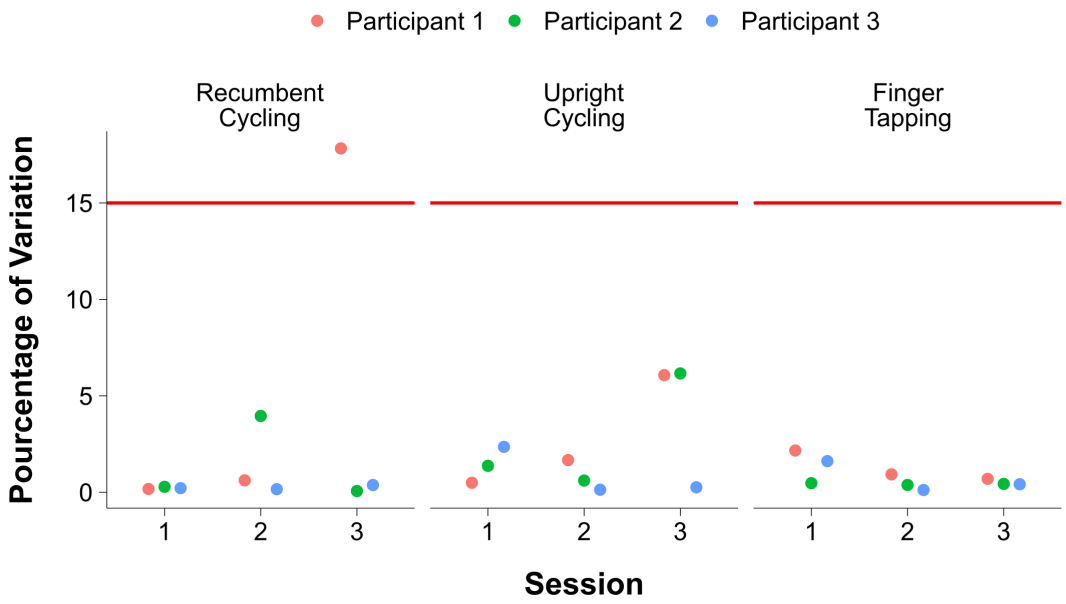
Figure 32

Behavioural Data for Each Session and Participant



Note. Mean IRI_{error} for each experimental condition and participant. Mean values are computed over 10 trials to highlight the distribution of IRI_{error} over the course of a session. Panel A: Data from Participant 1. Panel B: Data from Participant 2. Panel C: Data from Participant 3. IRI = inter-response interval; recumbent = recumbent cycling; upright = upright cycling; tapping = finger tapping.

Figure 33
fNIRS-Headset Shifts



Note. Variation of the *f*NIRS-head positioning for each experimental condition and participant. The red line indicates the *f*NIRS-headset shift threshold.

7.3.3 *Number of Trials*

To examine the robustness of the haemodynamic response of the brain during motor paradigms, $\bar{\Delta}_{HbO_2}$ was averaged over three randomly-selected successive trials for each task and participant. Then, the mean and standard deviation of $\bar{\Delta}_{HbO_2}$ were computed over 3, 10, 20, 30, 40, and 50 trials.

7.3.3.1 *Randomly-Selected Trials*

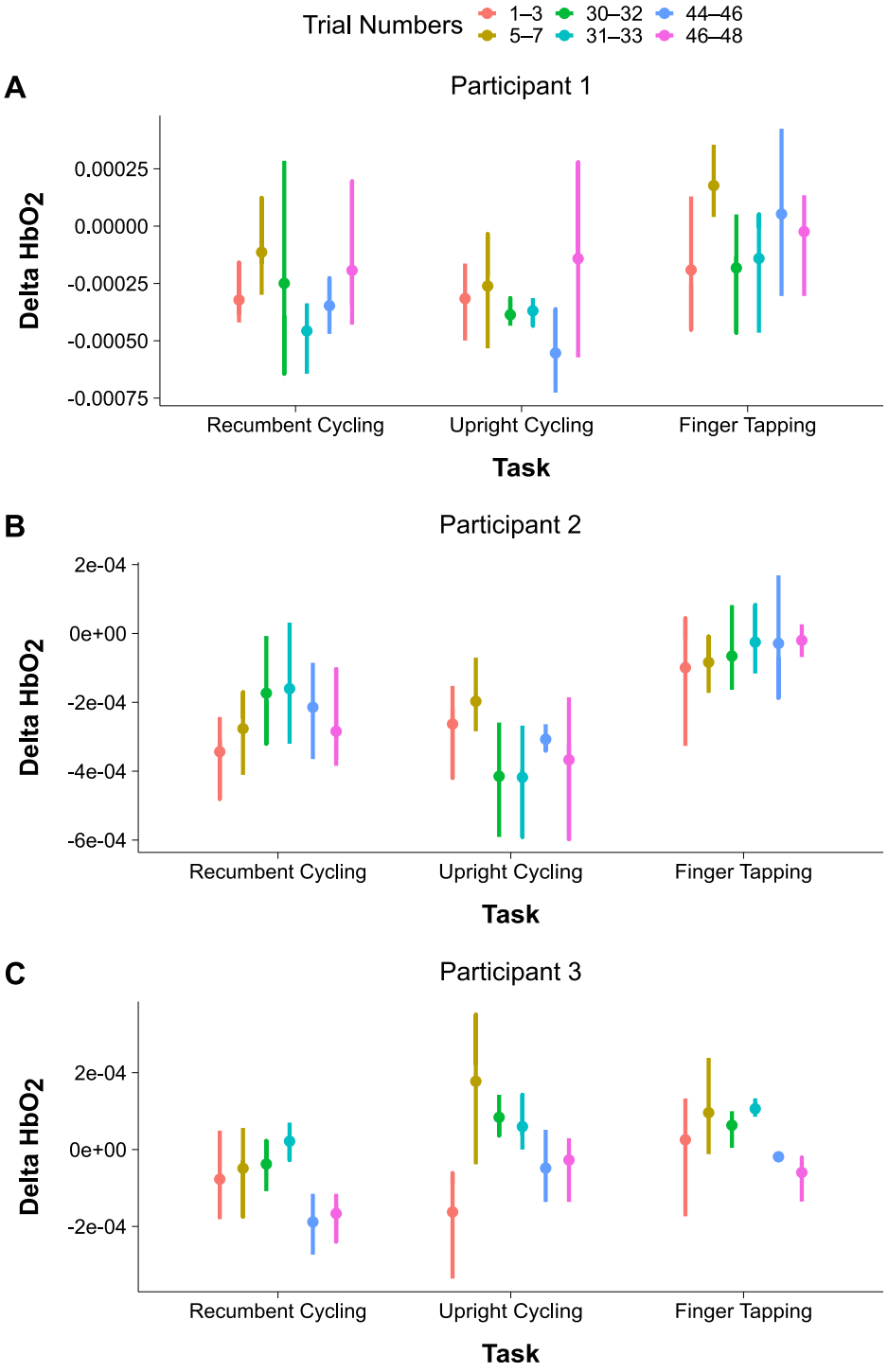
The results are presented in Figure 34. Collectively, the data from the three participants showed that, for the same experimental condition, $\bar{\Delta}_{HbO_2}$ values fluctuate depending on the selected cluster. Nonetheless, a common pattern arises when contrasting the three tasks. As an example, the haemodynamic responses of Participant 2 appeared to be invariably larger for the finger-tapping task when compared to the upright-cycling task (see Figure 34, Panel B).

7.3.3.2 *Incremental Number of Trials*

The results are presented in Figure 35. Taken collectively, the data showed that mean $\bar{\Delta}_{HbO_2}$ is stabilised after 10 trials in most experimental condition and participant (5 cases over 9; see Figure 36). Similar results were found for the mean standard deviation (4 cases over 9). It is worth noting that in several instances, the mean $\bar{\Delta}_{HbO_2}$ standard deviation seemed to increase over time (see Figure 35, Panels A and B, right side).

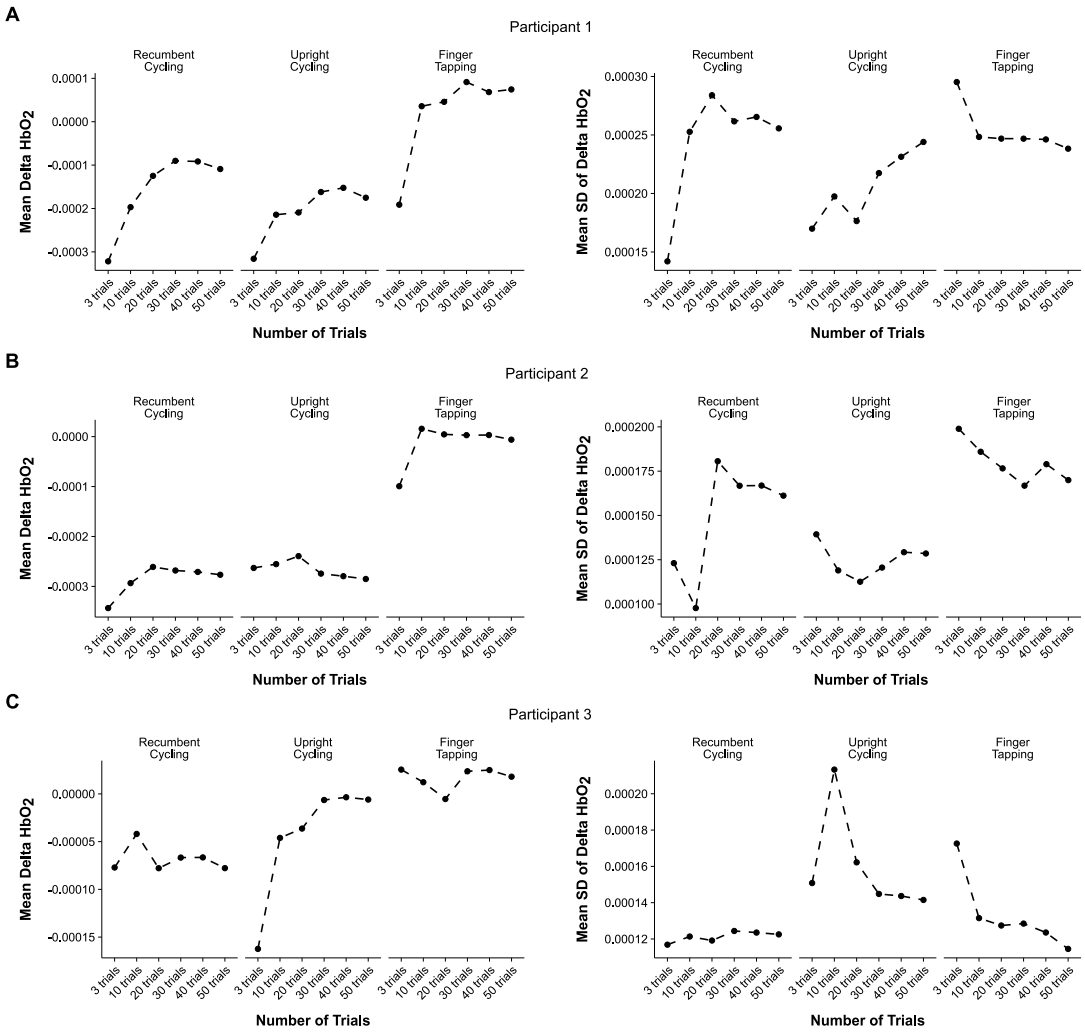
Figure 34

fNIRS Data for Several Clusters of Three Randomly-Selected Successive Trials



Note. Mean $\bar{\Delta}_{HbO_2}$ for each designated task and cluster of trials. The clusters of three successive trials were randomly selected among the 50 trials. Each line represents the data range (i.e., from minimum to maximum value). Panel A: Data from Participant 1. Panel B: Data from Participant 2. Panel C: Data from Participant 3.

Figure 35
fNIRS Data for Incremental Number of Trials

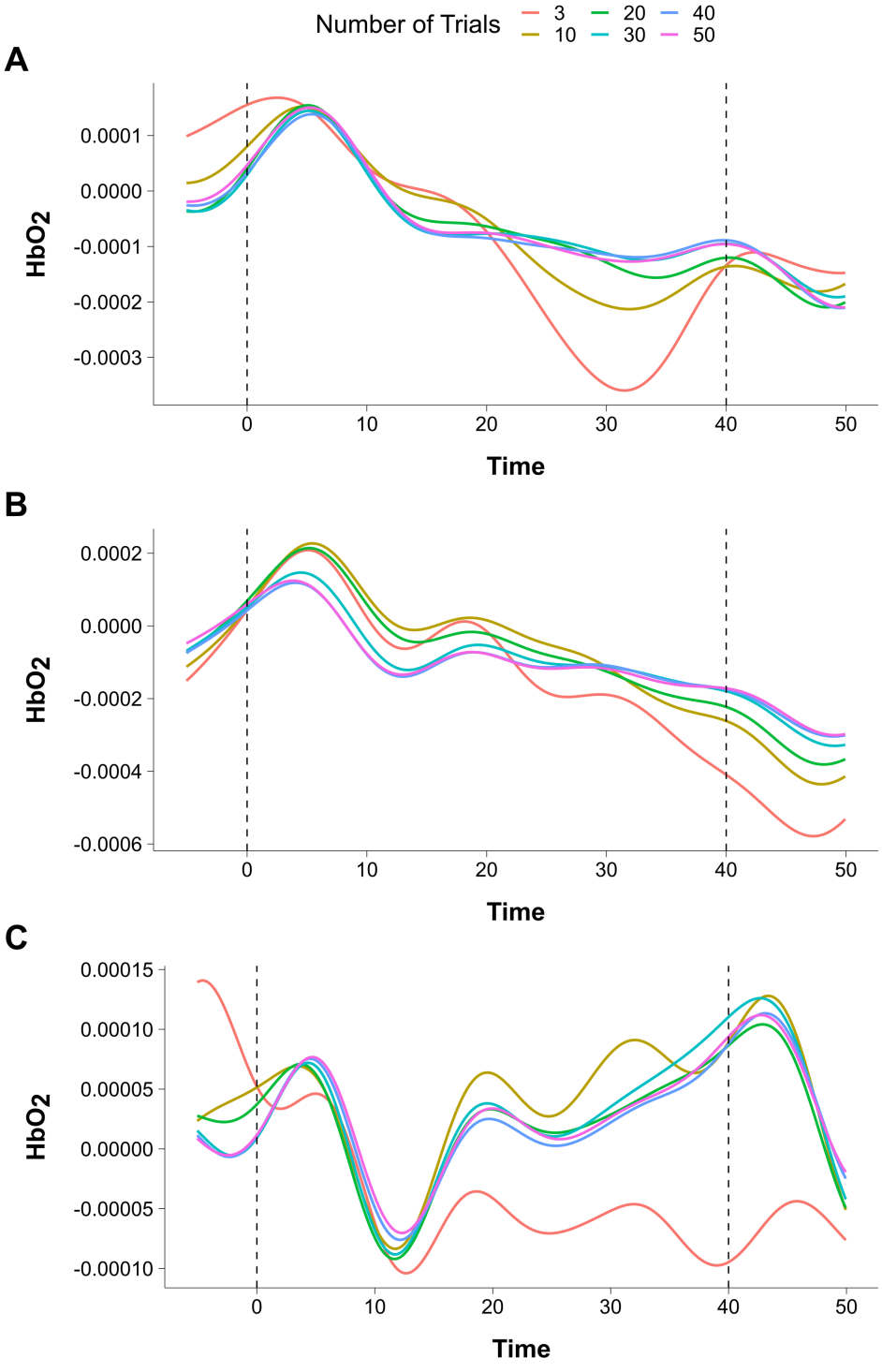


Note. Mean $\bar{\Delta}_{HbO_2}$ (left side) and mean standard deviation (right side) for each experimental condition and participant. Values are averaged over 3, 10, 20, 30, 40, or 50 trials. Panel A: Data from Participant 1. Panel B: Data from Participant 2. Panel C: Data from Participant 3. SD = standard deviation.

7.3.4 *Test–Retest Reliability*

To examine the test–retest reliability of *f*NIRS signals, RM ANOVAs were first performed for each participant; $\bar{\Delta}_{HbO_2}$ averaged over the 50 trials were used to achieve sufficient statistical power. Then, Pearson correlation coefficients were computed on the mean haemodynamic time course averaged over the 50 trials.

Figure 36
Mean Haemodynamic Time Course



Note. Data from Participant 1. Panel A: Mean HbO_2 for the recumbent-cycling task. Panel B: Mean HbO_2 for the upright-cycling task. Panel C: Mean HbO_2 for the finger-tapping task.

7.3.4.1 *RM ANOVAs*

For Participant 1, the RM ANOVA showed a significant main effect of task, $F(2, 98) = 12.47$, $p < .001$, $\eta_p^2 = .20$, with larger $\bar{\Delta}_{HbO_2}$ in the tapping ($M =$, $SD =$) than in the recumbent ($p < .001$) and upright-cycling tasks ($p = .042$). The main effect of session was non significant, $F(1.7, 83.19) = 12.47$, $p = .333$, $\eta_p^2 = .01$. The Task $\times$ Session interaction was significant, $F(4, 196) = 7.36$, $p < .001$, $\eta_p^2 = .13$, indicating that lower $\bar{\Delta}_{HbO_2}$ for the first vs. second ($p = .044$) and third sessions ($p < .001$) during the upright-cycling task and larger $\bar{\Delta}_{HbO_2}$ for the first vs. third session during the finger-tapping task ($p = .007$; see Figure 37, Panel A, left side).

For Participant 2, the RM ANOVA showed a significant main effect of task, $F(2, 98) = 78.27$, $p < .001$, $\eta_p^2 = .61$, with larger $\bar{\Delta}_{HbO_2}$ in the tapping than in the recumbent ($p < .001$) and upright-cycling tasks ($p < .001$). The main effect of session was also significant, $F(2, 98) = 24.80$, $p < .001$, $\eta_p^2 = .34$, indicating larger $\bar{\Delta}_{HbO_2}$ for the third session when compared to the first ($p < .001$) and second sessions ($p < .001$; see Figure 37, Panel B, left side). The Task $\times$ Session interaction was non significant, $F(4, 196) = 2.36$, $p < .055$, $\eta_p^2 = .05$.

For Participant 3, the RM ANOVA showed a significant main effect of task, $F(2, 98) = 38.18$, $p < .001$, $\eta_p^2 = .44$, with lower $\bar{\Delta}_{HbO_2}$ in the recumbent-cycling task than in the finger-tapping ($p < .001$) and upright-cycling tasks ($p < .001$; see Figure 37, Panel C, left side). The main effect of session was non significant, $F(2, 98) = 1.38$, $p = .256$, $\eta_p^2 = .03$. The Task $\times$ Session interaction was also non significant, $F(4, 196) = 1.55$, $p = .190$, $\eta_p^2 = .03$.

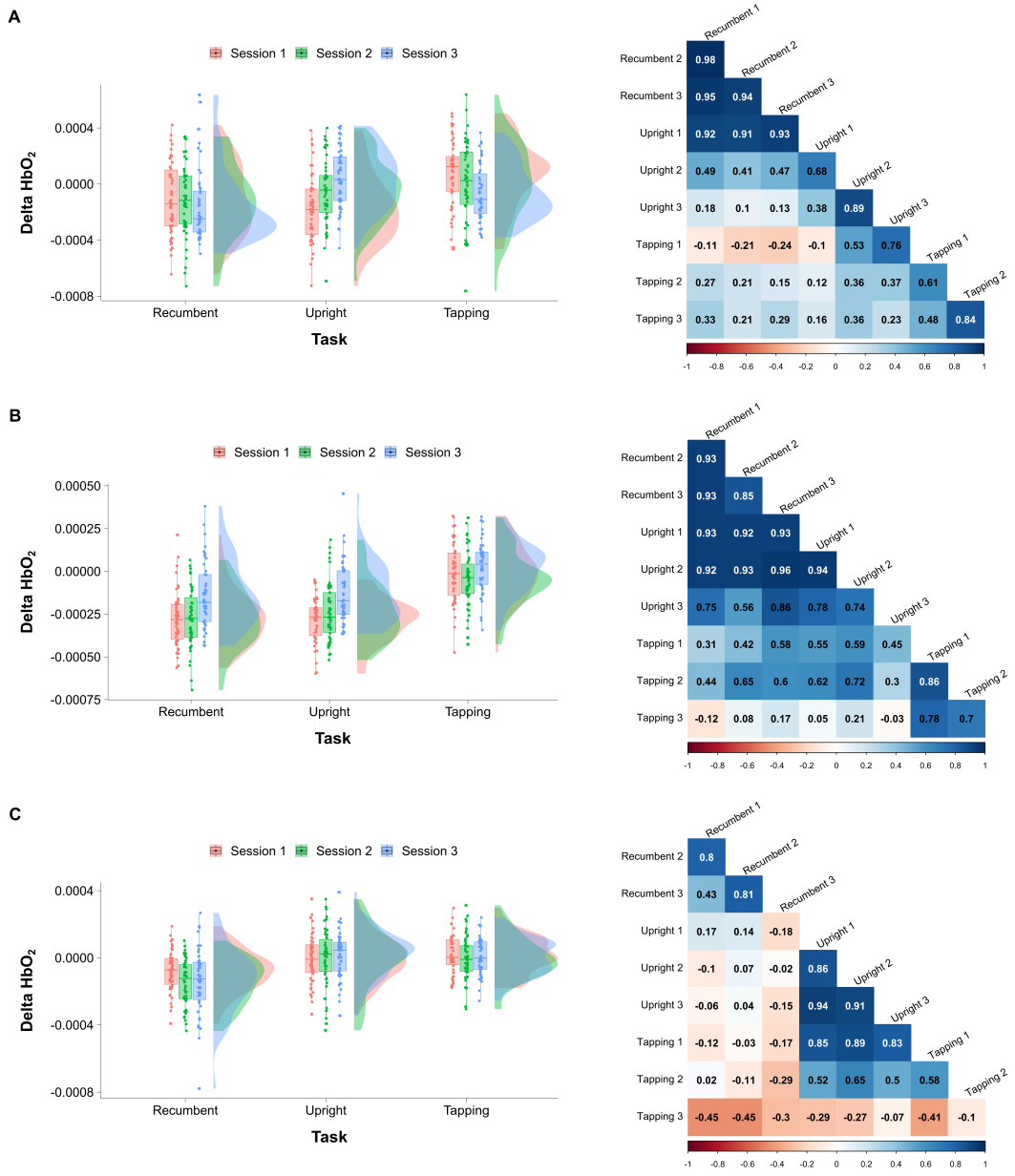
7.3.4.2 *Pearson Correlations*

The correlation matrix for each participant is presented in Figure 37. For Participant 1, very high positive correlation coefficients ($r > .90$) were found among the three sessions of the recumbent-cycling task. The finger-tapping and upright-cycling sessions were less positively correlated among them, with notable exception of the second and third sessions ($r_{tapping} = .84$, $r_{upright} = .89$). It is note worthy that the first session of the upright-cycling task was also highly positively correlated with the three recumbent-cycling sessions ($r > .90$).

For Participant 2, the positive correlation coefficients among the three sessions were high for the three tasks ($r_{recumbent} > .85$, $r_{upright} > .70$, $r_{tapping} > .70$). In addition, the mean haemodynamic time course was highly positively correlated among the two cycling tasks, regardless of the session (see Figure 37, Panel B, right side).

For Participant 3, high positive correlation coefficients ($r > .80$) were found among the first and second sessions of the recumbent-cycling task. The upright-cycling sessions were also highly positively correlated among them ($r > .85$). Only the first and second sessions of the finger-tapping tasks were found to moderately positively correlate ($r = .58$). It is worth mentioning that, for the finger-tapping task, the second and third sessions did not correlate, and the first and third session showed a small negative correlation ($r =$ -0.41)

Figure 37
Pearson Correlation Matrices



Note. Mean $\bar{\Delta}_{HbO_2}$ for each designated task and session (left side) and correlation matrix among experimental conditions (right side). Panel A: Data from Participant 1. Panel B: Data from Participant 2. Panel C: Data from Participant 3. Recumbent = recumbent cycling; upright = upright cycling; tapping = finger tapping.

7.4 DISCUSSION

The present study had several aims. The first one was to define the appropriate number of trials necessary to obtain a robust haemodynamic response using *f*NIRS. Test–retest reliability of the *f*NIRS results over several days was also performed at the within-subject level. Finally, the third aim was to prove the necessity to monitor the stability of the *f*NIRS headset over an experimental session using whole-body movement tasks. Three participants were asked to execute movements at close-to-spontaneous pace (i.e., 600 ms) during a SMS paradigm. For each motor task (i.e., finger tapping, recumbent cycling, upright cycling), three sessions of 50 trials that took place on different days were performed. The data analysis was conducted following a case-study procedure.

7.4.1 *fNIRS-Headset Shift*

An original contribution of the present study was to track the exact position of the *f*NIRS headset in relation to the participant's head over the course of a motor task. To that end, I take advantage of the optical motion capture technology, which is widely used in sport sciences and gait analysis (for a review, see Adesida et al., 2019). Motion capture is indeed originally employed to record the 3D-space coordinates of movements, which are then used to extract kinematic information such as speed, velocity, and jerk.

In the present study, a Qualisys motion-capture system has been twisted from its initial purpose and was used to record the Cartesian coordinates of three passive markers taped to the participant's temple and the *f*NIRS headset. The system used facilitated a temporal precision of 250 Hz and a spatial accuracy of < 0.2 mm. This innovative usage of the motion capture technology enabled the detection of any shift in the *f*NIRS-headset placement by comparing the position of the three markers between the beginning of the experimental session and any moment in time throughout this session.

The results of the present study showed that the *f*NIRS-headset placement was barely altered from the beginning vs. end of the experimental session (see Figure 33). Notably, the recorded variation seemed to be lower for the tasks in which the torso was stabilised (i.e., finger tapping and recumbent cycling). Relatively to the analyses executed in Chapters 4 and 6, an important examination of the present study was to verify the absence of *f*NIRS-headset shift *throughout* the entire experimental session. The findings showed that the *f*NIRS-headset positioning remained stable over the course of the experimental session (see Table 10). Thus, the motion-capture approach used allows to confirm that properly brain-located *f*NIRS data can be collected using whole-body movement paradigms.

An *f*NIRS-headset shift was, nonetheless, detected during one experimental session. Notably, this shift occurred in the recumbent-cycling condition, which was supposed to be more stable in terms of head movements than the upright-cycling. Researchers need to be very careful that the cranio-cerebral correlates of the NIR channels remain unaltered when conducting experimental studies with motor paradigms – even with tasks that do not induce much head movements. Thus, it is highly recom-

mended to always check the absence of *f*NIRS-headset shift, regardless of the motor task(s) employed.

7.4.2 *Stabilisation of The Haemodynamic Response*

When *f*NIRS experiments are predicated on a block-design procedure, the rule of thumb is to average the signal across three trials (see Menant et al., 2020). Results of the present study indicated that three trial were sufficient to capture the overall pattern of haemodynamic responses caused by movement execution. For illustrative purposes, the mean haemodynamic response of Participant 2 was always greater during the finger-tapping task when compared to the two cycling tasks. This pattern of results is true irrespective of the selected trials (see Figure 34).

Averaging only three trials led, nonetheless, to a cerebral response that was rather inconsistent at the intra-session level. Notably, the observed fluctuations in HbO_2 concentration due to the same experimental manipulation were found to be positive or negative depending on the selected trials (see Figure 34). While this seems to be especially the case for the upright-cycling condition, such inconsistency was also evident in more steady motor tasks (e.g., finger tapping). The lack of fidelity in the *f*NIRS responses can be problematic for researchers examining fine cognitive processes with tiny differences between experimental groups (e.g., language processing, visual perception).

The present preliminary analyses showed that averaging only three trials led to a mean haemodynamic response that could be very different from the response obtained with 50 trials (see Figure 36, Panels A and B). Nonetheless, a stabilisation of the mean haemodynamic response was observed as of 10 trials, with tiny variations from 10 to 50 trials. It is worth noting that the stabilisation of the response was observed only when brain oxygenation reached a plateau (i.e., from ~20 s). In the early stage of a motor task, the haemodynamic response was not affect by the number of trials averaged. In conclusion, 10 trials seem necessary to achieve a stable haemodynamic response of the brain in most participants and experimental conditions.

This number was, however, larger for the motor task engaging movement of the torso (i.e., upright cycling). In this situation, 20 trials seemed necessary to minimise the variability of both the means and the standard deviations of the haemodynamic responsess (see Figure 35). This could be due to signal contamination by motion artefacts (i.e., decoupling between the optodes and scalp), which are more prevalent when the motor task induces head movements (Vitorio et al., 2017). Thus, studies involving whole-body movement paradigms necessitate more trials than studies in which the chest is stable in order to ensure the validity of the obtained *f*NIRS data.

7.4.3 *Test–Retest Reliability*

Preliminary results of the present study showed that the test–retest reliability of the *f*NIRS signals was very good, especially for the recumbent-cycling (M_r[1] = .85) and upright-cycling tasks (M_r = .79). The finger-tapping task benefited from lower correlation coefficients (M_r = .60) that were completely equal to those reported in the

1 This corresponds to the mean correlation coefficient calculated over the three sessions and participant.

literature for finger-tapping paradigms (r = .60 on eight-block average; Strangman et al., 2006). Collectively, the present data indicated that the *f*NIRS technique benefits from a similar level of test–rest reliability than *f*MRI (see Yetkin et al., 1996) for single-effector movements.

The *f*NIRS test–rest reliability was higher when considering whole-body movements. This suggests that the *f*NIRS signals are less subject to day-to-day variation during whole-body vs. single-limb motor tasks. We can not exclude that the inter-session fluctuations observed for the finger-tapping task is due to small variation in the exact position of the optodes, arranged on the participant's head following the International 10–20 system guidelines (Jasper, 1958). Because whole-body movements recruit larger neural populations in the motor cortex (because of the motor homunculus), they would be less sensitive to slight variations in the optodes placement. Future research should aim to examine the test–rest reliability of *f*NIRS signals using an advanced neuronavigational approach to thoroughly control the optodes placement (e.g., 3D neuronavigation device; Machado et al., 2018).

It is note worthy that within a same motor task, the test–rest reliability was occasionally very high between two sessions but not among the three (see Figure 37, right side). Because the *f*NIRS signals are affected by physiological changes, the day-to-day variability in the haemodynamic response may be due to fluctuations in the individuals' physiology (e.g., body temperature, alertness; Blanco & Valdés, 2004; Mulderink et al., 2002). Even if the room climate and the caffeine consumption was thoroughly controlled in the present study, slight changes in individual physiology due to other sources of variation cannot be dismissed. By way of illustration, fatigue and calorie intake were found to alter a range of physiological indices (e.g., body temperature, heart rate; Soare et al., 2011; Tran et al., 2009). Thus, particular attention need to be given to the spontaneous fluctuations of physiological indices when designing and interpreting the results of *f*NIRS studies.

7.4.4 *Conclusions*

The findings of the present chapter make a substantial contribution to the existing *f*NIRS literature by advocating that at least 10 trials are necessary in a block-design procedure to obtain a robust haemodynamic response. In addition, the test–retest reliability of the *f*NIRS signals was high, even during whole-body movement motor paradigms. Finally, the monitoring of the *f*NIRS-headset positioning is highly recommended when conducting *f*NIRS studies involving body movements. While *f*NIRS brain imaging provides the researchers with the means to record cerebral activity of moving individuals, methodological precautions must be taken to ensure the validity and reliability of the collected data.

Part IV

GENERAL DISCUSSION

8

DISCUSSION

8.1 OVERVIEW OF THE PRESENT PROGRAMME OF RESEARCH

8.1.1 *My Initial Theoretical Perspective*

The human mind is characterised by two types of thinking. System 1 is fast and automatic, while System 2 is slow and requires effort. System 1 is used for ordinary, routine situations; when things get complicated, System 2 takes over and assigns attentional control to behaviours. Such a dichotomy allows individuals to minimise cost and maximise performance of cognitive and motor tasks. Notably, individuals are able to shift from System 1 to System 2 *modus operandi* (and vice versa) depending on the complexity of the situation in which they find themselves. Nonetheless, behaviours are executed either by System 1 *or* System 2 operations at a specific moment in time.

Emergent timing is the timing mode used when individuals perform actions using System 1. This timing mode depends on the mechanical, implicit emergence of temporal regularities from the kinematic parameters of movements. In contrast, predictive timing is implemented for actions performed under the cognitive wings of System 2. Here, movement timing originates from an explicit representation of time that requires attentional resources. These two timing modes are mutually exclusive and characteristic of fast and slow movements, respectively.

Emergent and predictive timing modes refer to timing strategies that are specific to two separate mental systems. Thus, it stands to reason that if the production of fast movement is supported by emergent timing and the production of slow movements by predictive timing, they should be underpinned by two distinct brain mechanisms. Specifically, fast-paced movements will depend on activation in motor areas, whereas slow-paced movements will be governed by prefrontal activity.

8.1.2 *Original Contribution of the Present Programme of Research*

The general aim of my thesis was to examine the cognitive and cerebral resources needed during the execution of voluntary movements performed under different time constraints. More precisely, both behavioural indices and brain signals were collected to test the hypothesis that slow-paced movements (< SMT) are underpinned by prefrontal cognitive control, whereas fast-paced movements (> SMT) are supported by motor automatic control.

Results of the present programme of work show that moving fast and slow entailed distinct timing strategies, with more feedback corrections (typical of predictive-timing mode) during slow-paced movements (see Section 3.2). In addition, the production of slow movements was characterised by greater attentional demands when compared to the production of fast movements (see Section 3.3). *f*NIRS evidence

indicated that upper-limb tasks performed at a fast pace relied on greater activity in the motor areas, whereas moving at a close-to-spontaneous pace exerted greater demand on the posterior prefrontal cortex (see Chapter 4).

Additional findings showed that single-limb and whole-body movements involved different timing strategies. They also showed that tapping-to-metronome paradigms might be too far removed from natural behaviours to facilitate translation of the results to everyday life motor activities (see Chapter 5). Making use of a paradigm that involves whole-body movements with concurrent *f*NIRS recordings, results indicated that slow pacing led to increased prefrontal activation (see Chapter 6). Similar activation did not manifest during single-limb movements.

Taken collectively, the findings emanating from the present thesis support the view that prefrontal and motor regions are differently engaged during the production of fast and slow voluntary movements. But does that necessarily imply that the brain generates fast and slow movements by use of two dedicated time mechanisms? Why is there a difference in cognitive and brain resources needed to move faster and slower than the spontaneous pace? More broadly, how does the brain encode and generate motor timing? In the following sections, I explore these questions and provide my view, in light of the results obtained during my 3-year programme of research.

8.2 TWO SYSTEMS FOR TIME PRODUCTION?

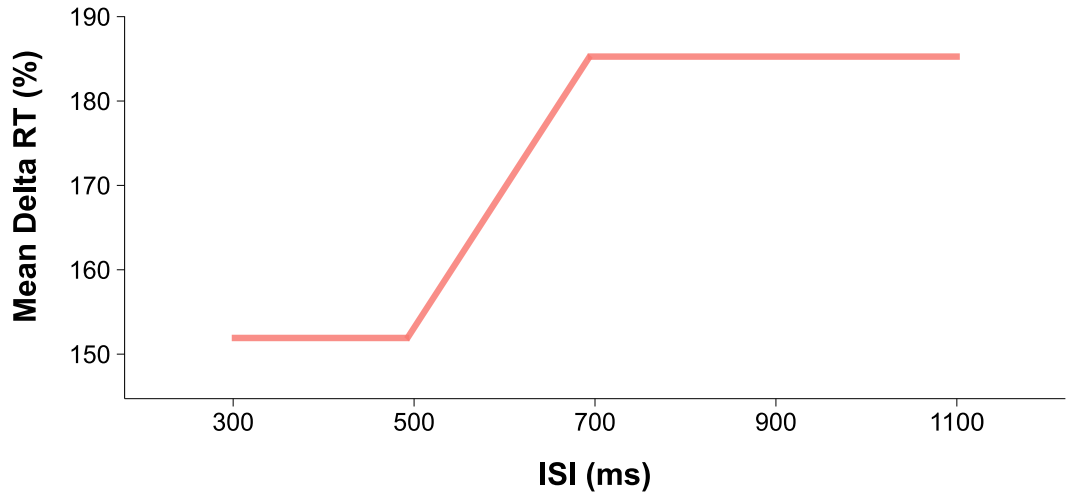
Recent advances in timing research suggest the coexistence of two timing mechanisms (automatic vs. controlled timing; Lewis & Miall, 2003a; Wiener et al., 2010a), which are adaptably engaged depending on the time-interval length being processed (Gooch et al., 2011; Wiener et al., 2011; Wiener et al., 2010b). The hypothetical division between these two timing mechanisms would lie at ~500 ms, which corresponds with the natural pace of human activities (i.e., SMT; Fraisse, 1982).

This coexistence hypothesis is congruent with the results of Chapter 3 showing an alternation between predictive and emergent timing modes as a function of externally-paced tempo. In addition, the production of slow movements was subject to greater cognitive control than the production of fast movements. Nonetheless, instead of a clear division around the SMT, data showed an inverse relationship between the cognitive resources required and motor pace. To put it another way, the slower an individual moved, the more attentional resources were required. If the production of fast movements is underpinned by System 1 (i.e., automatic, emergent timing) and the production of slow movements by System 2 (i.e., controlled, predictive timing), one would have expected to find an absence vs. presence of cognitive demand as a function of motor pace. The dual-task results, however, exhibited a smooth trend line in terms of the required cognitive resources, with no identifiable spike that would be indicative of a switch from System 1 to System 2 for movements executed at slow pace (see Figure 38).

The results of Chapter 3 showed that, when producing simple motor behaviours, slow movements were more prone to cognitive monitoring than fast movements. Nonetheless, the production of fast movements also engaged significant attentional resources as far as more complex motor actions were concerned. Within the two-

Figure 38

Schematic Representation of Expected vs. Actual Findings for the Dual-Task Study (Section 3.3)



Note. Expected findings for the one-target condition are displayed in red and actual (simplified) findings in blue. RT = reaction time; ISI = inter-stimuli interval.

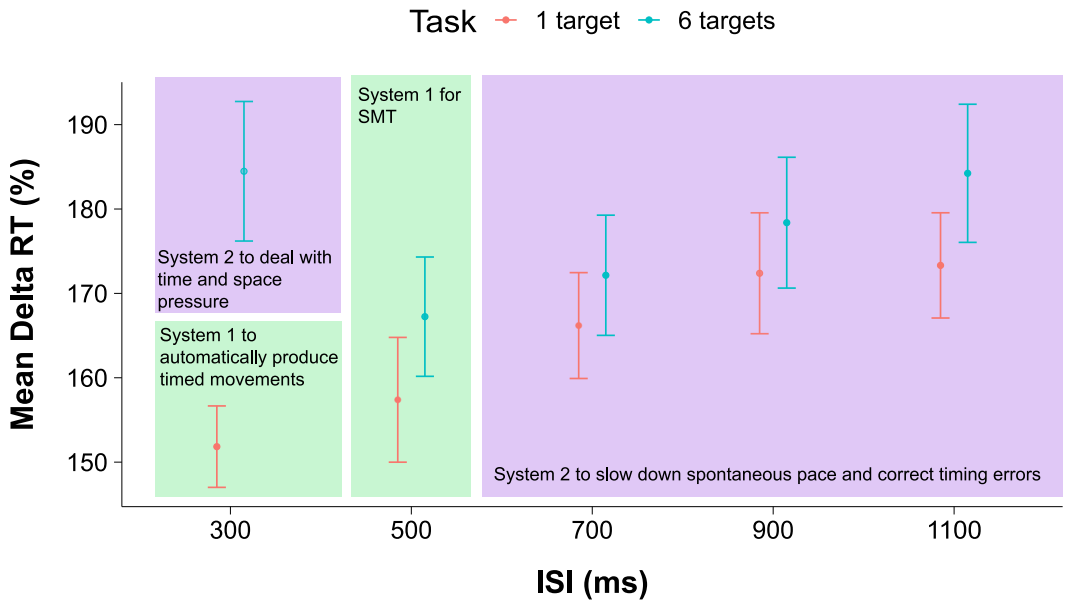
system approach of cognition, this suggests that System 1 underpins the execution of fast, simple movements as well as close-to-SMT simple and complex movements; System 2 is mobilised during the production of fast, complex movements along with slow, simple and complex movements. Thus, when examining the big picture, it is challenging to construct a coherent story from this Tetris-like configuration of System 1 and System 2 engagement (see Figure 39).

Rather than a fast vs. slow movement dichotomy, each time interval seems to have its own requirement in terms of the cognitive resources needed. This notion is congruent with the findings of Wright et al. (1997), who trained participants to discriminate intervals of 100 ms for 10 days. The authors showed that practice led to significant improvements in the discrimination of the 100-ms intervals, but no generalisation was found to the untrained intervals of 50 and 200 ms, even though they all represent fast-pace intervals. If every fast-pace interval emanates from the same general System 1 operations, the training of these operations on a particular fast interval should have improved the discrimination of all the other fast intervals.

The absence of generalisation to untrained time intervals has been replicated in several studies (see Bueti & Buonomano, 2014). It is worth mentioning that similar results were also found using interval reproduction, with generalisation only to close neighbouring time intervals (Bartolo & Merchant, 2009). The authors suggested that their findings support the existence of neural circuits tuned to specific time intervals. Such *neural tuning* was indeed highlighted during finger-tapping tasks in the putamen and SMA of monkeys (Merchant et al., 2013, 2015).

Taken collectively, the results of my thesis along with data from the scientific literature support the view that the existence of two timing mechanisms, one for

Figure 39
The "Big Picture" of System 1 and System 2 Operations



Note. System 1 operations are displayed in green and System 2 operations in violet. RT = reaction time; ISI = inter-stimuli interval; SMT = spontaneous motor tempo.

the production of movements slower than the SMT (regardless of the exact time interval) and one for those faster (again, regardless the exact time interval), is rather unlikely. It is note worthy that this theoretical position is driven only by *external* indices derived from individuals' behaviours (e.g., reaction time, timing variability). To understand the rules that govern motor timing, I started taking into account the *internal* indices of behaviour.

8.3 LINKING STRUCTURE AND FUNCTION

Each human behaviour mobilises a defined set of nerve cells. Examination of this neural activity provides valuable insight regarding brain function with reference to a given behaviour (Changeux, 1983). Functional neuroimaging techniques afford researchers with a means by which to link a particular behaviour with localised brain activity. That is, they offer a detailed view from the inside of the "black box" that has long been the brain metaphore.

In the studies pertaining to my thesis, I focused on motor regions because fast-paced behaviours were hypothesised to rely on body dynamics, and prefrontal regions because slow-paced behaviours were supposed to depend on a conscious representation of time that involves working memory and attention. Thus, I designed an *f*NIRS model that covered the dorsolateral prefrontal and orbitofrontal cortices, premotor cortex and SMA, and primary motor cortex over both brain hemispheres. This enabled me to examine the concurrent haemodynamic activity of several brain areas

with a spatial precision of ~1 cm. Because of this fine spatial precision, the recorded cortical activity was additionally split between right- and left-brain hemispheres.

Using this multi-channel *f*NIRS model, I showed that fast-paced movements induced higher motor activity when compared to slow-paced movements (Chapter 4). In addition, the production of slow-paced movements led to larger increase in the left-dorsolateral prefrontal and bilateral orbitofrontal cortices than the production of fast-paced movements (Chapter 6). Notably, no significant differences were found between the production of fast and close-to-SMT movements in both studies. Nonetheless, when looking at the figures, there seems to be a gradation in the prefrontal and motor haemodynamic responses from fast-to-slow tempi (prefrontal = slow > close-to-SMT > fast, motor = fast > close-to-SMT > slow ; see Figures 17 and 28).

Two hypotheses can be advanced to explain such an absence of significant differences in brain oxygenation between fast and close-to-SMT movements. First, it is possible that this particular contrast lacked statistical power. The required sample size was, however, carefully computed prior to data acquisition for each study (see Subsection 2.2.1). It could also be that the variation in cortical activity between the two experimental conditions is subtle and the *f*NIRS technique does not offer the level of fidelity to detect such a difference.

Collectively, the *f*NIRS findings pertaining to the present thesis support the notion for the existence of an equilibrium between prefrontal and motor brain activation. When individuals produce motor behaviours at SMT, prefrontal and motor cortical activation seem to be balanced and highly correlated (see Figure 30). This symmetry is broken when individuals deviate from their SMT, with a dominance of motor activity for fast-paced movements and of prefrontal activity for slow-paced movements.

It is arguable that prefrontal and motor brain areas are strongly connected from a functional perspective for the timing of motor behaviours. Empirical data support the existence of modulatory signals from prefrontal cortex to motor regions during action selection (Hasan et al., 2013; Rowe et al., 2005). In addition, Rowe et al. (2002) showed a reduced connectivity from prefrontal cortex to SMA in patients with Parkinson's disease; it was proposed that this finding reflects impaired attention to action production (see Jueptner et al., 1997). Hence, signals emanating from the prefrontal cortex would be of particular importance to the appropriate timing of motor behaviours.

Evidence emerging from the neuroimaging field has suggested that prefrontal–motor connectivity is crucial for successful inhibitory control (Picazio et al., 2014; Rae et al., 2015). Within the context of motor timing, it is thus plausible that prefrontal regions send inhibitory signals to the motor areas in order to slow the pace of motor execution – namely to *inhibit* the urge to move at spontaneous pace. This would provide a strong explanation for the reduced motor activity observed when prefrontal activity is important. Such a notion implies that the motor areas have the capacity to deal with the timing aspect of movement. More precisely, motor timing would be embedded within the motor regions of the brain.

8.4 TIMING AS AN EMERGENT PROPERTY OF NEURAL NETWORKS

Population-clock models posit that timing is an intrinsic property of neural networks. This implies that the activity of a single neuron is uninformative but the activity of an entire neuronal population provides valuable information pertaining to time. An interesting implication of population-clock models is that, in essence, *every* cortical circuit is able to code time through time-dependent changes in the neural-network state (Buonomano & Karmarkar, 2002). For a particular task, the location within the brain of the neural network coding time is dependent upon the nature of the task (e.g., motor neurons for a motor-timing task, visual neurons for a visual-temporal discrimination task; Buonomano, 2017).

Both time perception and production are assumed to depend on the activity of population-clock networks (Buonomano & Laje, 2011). Nonetheless, the neural networks coding for time production are characterised by strong and recurrent synaptic connections that allow self-sustaining activity to take place. Thus, motor timing could well be embedded in the cerebral cortex, the most likely candidate being the motor regions (Buonomano & Laje, 2011; Buonomano & Maass, 2009).

Within the population-clocks framework, the pace of motor behaviours is encoded in the speed of neural trajectories (i.e., the complex and time-varying pattern of neural-population activity in the neural space). Notably, a specific neural trajectory corresponds to a particular behaviour, which implies that "producing the same motor pattern slowly or quickly may rely on very similar neural trajectories evolving at a fast or slow speed, respectively" (Paton & Buonomano, 2018, p. 699). A correlation was indeed found between the timing of a neural trajectory and the associated motor response (e.g., fast neural trajectories produced fast motor responses; Paton & Buonomano, 2018). Thus, motor timing appears to emerge from the dynamics of neural networks. This led Buonomano (2017) to state that:

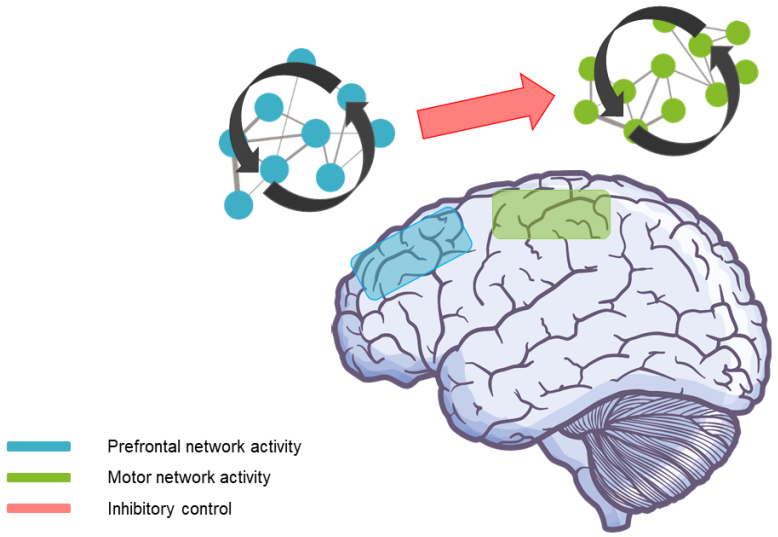
> Each synapse and each [...] neuron contributes to the pattern, but no single synapse or neuron is actually necessary. The pattern is an *emergent* property: *the whole is larger than the sum of the parts*. (p. 123)

The firing of a neuron – or a population of neurons – engenders an energy cost that must be balanced by nutrient intake in terms of oxygen and glucose (Magistretti et al., 1999). The rate of neuronal activity is known to be positively correlated with local oxygen consumption (Özugur et al., 2020). Accordingly, the larger haemodynamic activity found over the motor cortex for fast and close-to-SMT vs. slow movements in Chapter 4 could be due to a higher rate of neuronal activity. More precisely, the production of slow and fast movements would have engaged the same motor neural network, but with differing rates of neural trajectory.

Such pace-dependent motor activity was not replicated in Chapter 6. Rather, the walking task led to greater oxygenation in the motor regions (i.e., primary motor cortex, premotor cortex and SMA) when compared to the drawing task. One possible explanation is that motor timing of whole-body movements involved larger neural networks than upper-limb movements; a notion consistent with the population clocks assumption that a given neural network is specific to a particular motor pattern (Paton & Buonomano, 2018). Thus, the massive neural recruitment typical of whole-body movements could have masked the more subtle effect of motor tempo.

Figure 40

Schematic Representation of the Brain Regions and Connectivity Involved in Motor Timing.



Note. Icons are sourced from John Chilton and Alexander Bates (SciDraw).

This assumption is supported by the fact that the effect size found for the task effect in Chapter 6 (η_p^2 = .47) was almost twice that associated with the tempo effect in Chapter 4 (η_p^2 = .28).

Karmarkar and Buonomano (2007) suggested that the population-clocks model is limited to time intervals below 500 ms. Longer intervals would be processed through a clock-like mechanism, which involves high-level cognitive processes (e.g., working memory; Lewis & Miall, 2003c; Treisman, 1963). In contrast, I propose that the production of timed motor behaviours, from hundreds of milliseconds to a few seconds, is underpinned by a unique process.

8.5 COGNITIVE CONTROL TO SLOW DOWN SPONTANEOUS PACE

The production of slow movements would rely on the same population clocks as the production of fast movements, but is additionally subject to cognitive monitoring in order to regulate the pace of motor execution. More specifically, prefrontal inhibitory signals are sent to the motor neurons in order to inhibit neural trajectories (see Figure 40). Previous research has shown that reducing the speed of neural trajectory in the premotor nucleus of songbird significantly decelerated song pace across various timescales (Long & Fee, 2008). Notably, the authors found that decreasing the speed of the motor nucleus did not significantly affect song pace. This finding suggests that the premotor area is the key location of motor-timing neural trajectories, while the motor region acts more as a vassal.

I propose that the number of cognitive resources required to perform a behaviour is proportional to the interval between the SMT and the pace of the current be-

haviour. More specifically, movements have an optimal, natural pace and an increasing amount of cognitive control is applied as they are slowed. That is, 700-ms actions are less subject to cognitive control than 900-ms actions, which are, in turn, less subject to control than 1100-ms actions. This notion provides a strong explanation to the smooth increase in attentional resources needed to perform a motor-task observed as the movement pace slowed in Chapter 3.

In the population-clocks model, a neural trajectory depends on the specific motor pattern that is performed (Buonomano & Karmarkar, 2002). The temporal structure for a given movement is not transferable to another movement. This assumption is congruent with the finding presented in Chapter 5, that timing performances were affected by the class of motor actions. Nonetheless, the brain mechanism for inhibiting spontaneous motor pacing should be observable whatever the nature of the movement that is executed.

In Chapter 6, I reported that slow-paced movements led to increased prefrontal activity during walking but not circle drawing. Thus, I suggested that the prefrontal inhibitory control would be magnified in the case of phylogenetically old motor behaviours such as locomotion. Locomotion is a stereotyped pattern of movements that is assumed to be generated by central pattern generators (CPGs) located in the brainstem and spinal cord (Steuer & Guertin, 2018). A CPG is a neuronal network in which interconnected excitatory and inhibitory neurons produce an oscillating, rhythmic output without the need for sensory feedback or other patterned input (Katz, 2016).

The oscillatory properties of CPGs emerge from the strength of synaptic connectivity within the network. More precisely, synaptic connections need to be particularly strong in order to maintain the oscillating pattern over time. Accordingly, CPGs might be a type of non-cortical population clocks. The neural trajectories underpinning the timing of locomotion would thus be localised in non-cortical regions (e.g., brainstem) whereas those of more cognitive motor behaviours would lie in cortical areas. A particularity of non-cortical population clocks could be that they are characterised by stronger synaptic weights when compared to that of surface layers of the brain. Thus, reducing the speed of locomotor-timing neural trajectories could necessitate strong inhibitory control from the prefrontal cortex in order to weaken the synaptic connections.

8.6 LIMITATIONS AND STRENGTHS OF THE PRESENT PROGRAMME OF WORK

8.6.1 *Limitations*

The present programme of research has several limitations that are worthy of note. Firstly, it would have been interesting to include several slow-paced conditions in the experimental design of my *f*NIRS studies. This would have enabled me to achieve a finer overview of the brain mechanisms involved in motor timing. Moreover, there is a possible gradation in prefrontal activation with the slowing of externally-paced tempo. However, the duration of the experimental sessions would have been dramatically increased, rendering such an approach impracticable.

It is arguable that the synchronisation tasks used in my experimental studies did not bear close resemblance to the requirements of everyday behaviours. More specifically, the precise synchronisation of motor behaviours with externally-paced tempo entails additional information-processing resources. Thus, synchronised movements could have involved slightly different brain processes when compared to self-paced movements (see Toyomura et al., 2012). Nonetheless, making use of a SMS paradigm enabled me to ensure that each participant performed motor behaviours at the same pace for each experimental condition.

It is important to highlight that the *f*NIRS headset was placed on each participant's head in accord with the International 10–20 system guidelines. Thus, the inter-individual variability in brain structure was not considered. This could have led to the averaging of haemodynamic responses that did not emanate from precisely the same brain location across participants. Nonetheless, activity from individual channels was averaged across cerebral regions-of-interest, thus reducing the influence of the inter-individual brain structure variability.

The lack of accessibility to subcortical regions owing to the nature of the *f*NIRS technique is duly acknowledged as a limitation. Subcortical regions such as basal ganglia and cerebellum were found to have a pivotal role in motor timing (see e.g., Buonomano & Maass, 2009; Paton & Buonomano, 2018, for reviews). It is worth mentioning that the first population-clocks model was actually proposed with reference to the cerebellum (Buonomano & Mauk, 1994). Nonetheless, the *f*NIRS technique is restricted to a recording depth of ~0.5–2.0 cm, which limits access to cortical brain activity.

8.6.2 *Strengths*

There are several strengths associated with the present thesis. The first is that I monitored brain, physiological, and behavioural indices concurrently. Recording HR and respiratory frequency allowed me to verify the quality of the obtained haemodynamic signals, which constitutes an important step in *f*NIRS data analysis (see Subsection 2.3.3). In addition, the dual collection of behavioural and brain imaging data enabled me to remove from the analyses the *f*NIRS data pertaining to trials characterised by less than 30% of behavioural accuracy. The combination of neuroimaging and behavioural evidence is essential to ensure that the participants performed the task correctly, and that the obtained brain pattern of activation is indicative of the behaviour of interest.

A strength of the present programme of research is that it provides some legitimacy for the use of *f*NIRS during whole-body movements. The scientific community presently lack validation studies regarding the use of *f*NIRS to measure brain functions during human locomotion. With the desire to address this methodological ellipsis, I developed an innovative procedure using 3D recordings to verify the absence of *f*NIRS-headset shift over the entire experimental session. In addition, I showed that an acceptable level of test–retest reliability is achieved in whole-body movement paradigms (Chapter 7).

The use of the *f*NIRS technique allowed me to record brain activity *during* whole-body motor tasks. Although some researchers have argued that the brain correlates

of time perception are similar to those of time production (Rubia & Smith, 2004; Schubotz et al., 2000), they examined brain activity though the application of *f*MRI during artificial motor tasks (e.g., finger tapping). Given that the *f*NIRS technique is less sensitive to motion artefacts, it represents a unique opportunity to gain fuller understanding of the brain mechanisms that underlie timing-related motor behaviours.

In the experimental studies of the present thesis, I endeavoured to use several motor tasks, all involving a particular form of movement (e.g., finger tapping, walking, cycling). Thus, I was able to examine the generalisability of the findings to a wide range of motor behaviours. This represents a move towards bridging the gap between laboratory tasks and daily living behaviours. Despite calls for such work, there has been a noticeable dearth of studies in the field of human neurosciences (Sonkusare et al., 2019).

8.7 MY CURRENT THEORETICAL POSITION

The production of slow movements relies on the same motor process as the production of fast movements. Slow-paced movements are, however, subject to additional cognitive activity in order to slow motor execution. The timing of motor actions is not underpinned by two distinct systems that are engaged in accord with an "on–off rule" depending on individual's resources and task constraints. Rather, the pace of motor behaviours emerges from the dynamics of a population of (pre)motor neurons, that I refer to as *reference state*. More precisely, neurons with strong synaptic connections produce self-sustained neural trajectories that are used as timers.

When individuals need to produce slower actions (with reference to the SMT), inhibitory control is applied to neural dynamics; motor behaviours are timed under a *supervised state*. Nonetheless, individuals do not *switch* their timing strategies when producing slow behaviours. Timed-motor actions still emerge from neural trajectories, but an additional cognitive, inhibitory control may be applied. However, scientists cannot "see" the emergent aspect of motor timing during the supervised state as it is hidden from their sight by the cognitive load set upon behaviours.

This view represents a parsimonious, unified model of motor timing. Rather than having two processes (automatic vs. controlled timing) that researchers have been struggling to conciliate for several decades, individuals would time their actions through a single motor mechanism that is more or less subjected to cognitive control.

In the years to come, I endeavour to pursue investigation of the neurocognitive mechanisms underlying the modulation of motor timing. A first line of research will consist in the use of functional connectivity to better understand the prefrontal–motor connection during the timing of motor behaviours. Furthermore, I will use artificial neural networks in order to model the processing of timed motor behaviour within the theoretical framework of population clocks. Finally, the causal effect of prefrontal inhibitory control on the deceleration of the motor network activity could be examined using repetitive transcranial magnetic stimulation.

Part V

APPENDICES

A

ETHICAL CLEARANCE

A.1 *f*NIRS STUDY OF CHAPTER 4

Université de Lille

Comité d'éthique en sciences comportementales

Président :
Yvonne DELEVOYE-TURRELL

Président adjoint :
Céline DOUILLIEZ

Personne ressource (dossier administratif) :
Aurélie DUCROQUET
Tél : 03.20.41.67.92 -
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Villeneuve d'Ascq le 14/12/2017

Références comité d'éthique :	**2017-1-S56**
Sigle :	**NIRS TAPPING**
Numéro de version et date :	**Version 1 DU 26/09/2017**
Promoteur :	**LILLE 3**
Porteur projet :	**Y.Delevoye, C.Roger, S.Guerin, N.Glinval**

Date de la soumission : **10/10/2017**

Date de la réunion du comité d'éthique : **14/11/2017**

Avis du comité d'éthique : **AVIS FAVORABLE SOUS MODIFICATIONS MINEURES**

Merci de faire parvenir au comité d'éthique, dans un délai de 3 semaines, le nouveau protocole (avec nouveau numéro de version et date correspondante) tenant compte des modifications demandées à l'adresse : ethique.administration@univ-lille3.fr ainsi qu'une lettre reprenant point par point les réponses apportées aux remarques du comité d'éthique afin d'y expliquer, le cas échéant, les changements apportés.

Passé ce délai, le protocole devra faire l'objet d'une nouvelle soumission.

Pr Yvonne DELEVOYE-TURRELL
Présidente du comité d'éthique

Y. Delevoye

A.2 BEHAVIOURAL STUDY OF CHAPTER 5

University of Hertfordshire UH

HEALTH AND HUMAN SCIENCES ECDA

ETHICS APPROVAL NOTIFICATION

TO Dr Dawn et al

FROM Dr Richard Southern, Health and Human Sciences ECDA Acting Chair

DATE 14/02/2017

Protocol number: aLMS/SF/UH/02547(1)

Title of study: Investigating the effects of audio,visual and audio-visual combination modalities on finger and toe tapping and marching 'on the spot' entrainment (ie synchronisation with external stimuli) in people with and without Parkinson's disease.

Your application to <extend and/or modify> the existing protocol as detailed below has been accepted and approved by the ECDA for your School and includes work undertaken for this study by the named additional workers below:

Modification: New location and new mode of data collection as per EC2

This approval is valid:

From: 14/02/2017

To: 31/10/2018

Additional workers: Dr Lucy Annett , Dr Peter Lovatt

Please note:

Any conditions relating to the original protocol approval remain and must be complied with.

Approval applies specifically to the research study/methodology and timings as detailed in your Form EC1 or as detailed in the EC2 request. Should you amend any further aspect of your research, or wish to apply for an extension to your study, you will need your supervisor's approval and must complete and submit a further EC2 request. In cases where the amendments to the original study are deemed to be substantial, a new Form EC1 may need to be completed prior to the study being undertaken.

Should adverse circumstances arise during this study such as physical reaction/harm, mental/emotional harm, intrusion of privacy or breach of confidentiality this must be reported to the approving Committee immediately. Failure to report adverse circumstance/s would be considered misconduct.

Ensure you quote the UH protocol number and the name of the approving Committee on all paperwork, including recruitment advertisements/online requests, for this study.

Students must include this Approval Notification with their submission.

A.3 fNIRS STUDIES OF CHAPTERS 6 AND 7

Université de Lille

Comité d'éthique en sciences comportementales

Président :
Yvonne DELEVOYE-TURRELL

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Villeneuve d'Ascq le 22/06/ 2018

Références comité d'éthique :	**2017 -8-S52**
Sigle :	**NIRS SENSATIONS**
Numéro de version et date :	**Version 4**
Promoteur :	**ULille SHS**
Porteur projet :	**Yvonne DELEVOYE**

Date de la soumission : **13/05/2018**

Date de la réunion du comité d'éthique : **21/06/2018**

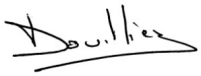
Avis du comité d'éthique : **AVIS FAVORABLE**

Le protocole est accepté en état. Si pour une quelconque raison, vous souhaitez modifier le protocole (en terme de calendrier, inclusion d'un nouveau groupe…), vous êtes tenu d'informer le comité d'éthique par l'envoi d'un avenant expliquant les motivations mais également les modifications apportées au protocole initial.

Cet avenant sera réévalué par le comité d'éthique.

La Vice-Présidente du comité d'éthique

Céline Douilliez



B

DEOXYGENATED HAEMOGLOBIN RESULTS FOR CHAPTER 6

The *f*NIRS dependent variable $\bar{\Delta}_{HHb}$ was analysed independently for each region of interest. A twoway RM ANOVA (Motor Tempo [300, 600, 1200 ms] × Task [drawing, walking]) was applied. Aberrant values (i.e., > Q3 + 3 × IQR[1] or < Q1 - 3 × IQR) were removed from the statistical analyses. Normality was checked using visual inspection of the quantile–quantile plots and the Shapiro–Wilk test. Where Mauchly's tests indicated violations of the sphericity assumption, Greenhouse–Geisser corrections were applied. Paired *t* tests with Bonferroni adjustements were used as post hoc tests where necessary.

B.1 ORBITOFRONTAL CORTEX

The RM ANOVA did not show a significant main effect of task, $F(1, 11) = 3.01$, $p = .111$, $\eta_p^2 = .21$, or motor tempo, $F(2, 22) = 0.64$, $p = .535$, $\eta_p^2 = .06$. The Task × Motor Tempo interaction was also non significant, $F(2, 22) = 0.620$, $p = .547$, $\eta_p^2 = .05$.

B.2 DORSOLATERAL PREFRONTAL CORTEX

The RM ANOVA did not show a significant main effect of task, $F(1, 9) = 0.51$, $p = .491$, $\eta_p^2 = .05$, or motor tempo, $F(2, 18) = 0.52$, $p = .602$, $\eta_p^2 = .06$. The Task × Motor Tempo interaction was also non significant, $F(2, 18) = 2.11$, $p = .150$, $\eta_p^2 = .19$.

B.3 PREMOTOR CORTEX AND SMA

The RM ANOVA did not show a significant main effect of task, $F(1, 9) = 0.192$, $p = .672$, $\eta_p^2 = .02$, or motor tempo, $F(2, 18) = 0.10$, $p = .908$, $\eta_p^2 = .01$. The Task × Motor Tempo interaction was also non significant, $F(2, 18) = 1.53$, $p = .243$, $\eta_p^2 = .14$.

B.4 PRIMARY MOTOR CORTEX

The RM ANOVA did not show a significant main effect of task, $F(1, 11) = 2.75$, $p = .126$, $\eta_p^2 = .20$, or motor tempo, $F(1.27, 13.99) = 0.70$, $p = .451$, $\eta_p^2 = .06$. The Task × Motor Tempo interaction was also non significant, $F(1.34, 14.73) = 1.92$, $p = .187$, $\eta_p^2 = .15$.

1 Interquartile range.

Science needs time to think. Science needs time to read, and time to fail. Science does not always know what it might be at right now. Science develops unsteadily, with jerky moves and unpredictable leaps forward – at the same time, however, it creeps about on a very slow time scale, for which there must be room and to which justice must be done.

— The Slow Science Manifesto

ACKNOWLEDGMENTS

Mes premières pensées vont au Pr Yvonne N. Delevoye-Turrell, ma directrice de thèse. Que de chemin parcouru depuis que je suis entrée dans votre bureau en cette fin d'année 2015 pour vous demander de me superviser pour mon travail de recherche de Licence 3... Pour rien au monde je ne changerais quoi que ce soit à ces six dernières années. En plus d'être une chercheuse et une enseignante accomplie, vous avez des qualités humaines qui font de vous quelqu'un de grand. Merci pour m'avoir donner la liberté et l'espace nécessaire pour grandir dans le monde impitoyable mais grisant de la recherche, tout en étant un phare dans la nuit vers lequel je pouvais revenir, à n'importe quel moment, pour obtenir des conseils toujours avisés. Pour m'avoir soutenue dans mes élans créatifs et mes prises de risque tout comme dans mon approche méthodologique quasi-rigide et mon entêtement à suivre à la lettre les règles APA (je sais que ça va vous manquer !). Pour être toujours prête à entamer de grandes discussions théoriques, même à 7h15 du matin autour d'un thé, tout comme à bavarder du contenu de notre week-end. Pour mettre du Jean-Jacques Goldman en fond lors de nos séances d'écriture. Vous êtes la meilleure directrice de thèse que j'aurais pu avoir – et je choisis mes mots avec soin. Pour tout, merci.

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le tableau blanc. De notre émotion à découvrir les traces d'une activation dans un signal. On forme une équipe de choc, aussi complémentaire que complice, et c'est sans aucun doute le secret d'une collaboration réussie – et d'une belle amitié. Merci d'avoir contribué à rendre inoubliables mes trois années de thèse.

C'est avec émotion que j'adresse mes plus sincères remerciements à la team FATAAL, et tout particulièrement au noyau dur : Yvonne (encore !), Victor P. M. Brossard et Adamantia Batistatou. Se sentir épaulée et soutenue par ses collègues est rare et précieux, surtout dans le monde compétitif de la recherche académique. Je mesure la chance que nous avons d'avoir réussi à construire un environnement de travail bienveillant et profitable à tous, au sein duquel chacun peut s'épanouir et profiter de l'expérience et des compétences des autres. Travailler à vos côtés, jour après jour, a été un véritable privilège et j'en garderai toujours un souvenir ému. Il y a eu du passage dans la team FATAAL depuis sa naissance en fin 2017, des étudiants qui sont venus, ont évolués, et sont partis voler de leurs propres ailes – et je veux remercier ici plus spécifiquement Diwan Lefebre, Simon Drosik, Wynona Wallart et Alizée Louizo, les étudiants que j'ai co-supervisés pour leur projet de recherche. Néanmoins, nous avons toujours réussi à faire perdurer la bonne humeur, l'ambiance créative et la rigueur scientifique qui sont le coeur de notre équipe. J'ai également une pensée pour notre adoptée FATAAL niçoise, Roxane L. Bartoletti, qui a été un petit rayon de soleil pendant les quelques mois qu'elle a passés à Lille dans le cadre de son indoc.

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