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The motor of time:

Coupling action to temporally predictable events heightens perception

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Field Code Changed

Abstract

Timing and motor function share neural circuits and dynamics, which underpin their close and synergistic relationship. For instance, the temporal predictability of a sensory event optimizes motor responses to that event. Knowing when an event is likely to occur lowers response thresholds, leading to faster and more efficient motor behavior though in situations of response conflict can induce impulsive and inappropriate responding. In turn, through a process of active sensing, coupling action to temporally predictable sensory input enhances perceptual processing. Action not only hones perception of the event's onset or duration, but also boosts sensory processing of its non-temporal features such as pitch or shape. The effects of temporal predictability on behavior involve motor and left parietal cortices and are mediated by changes in delta and beta oscillations in motor areas of the brain.

Introduction

Estimating the duration of an event engages regions of the brain traditionally associated with motor function, such as Supplementary Motor Area, basal ganglia and cerebellum, even when the temporal estimation process is purely perceptual (Wiener et al, 2010; Naghibi et al, 2023). This neuroanatomical overlap suggests that timing might share functional mechanisms with motor processing, and that we may even acquire our sense of time through action (Coull and Droit-Volet, 2018). The inherent link between temporal processing and motor systems is exemplified by the universal and innate act of dancing to the beat of music (Mehr et al., 2019). While music is most often considered an auditory phenomenon, from an ecological and phylogenetic perspective it is tightly coupled to dance (Fitch, 2016). This uniquely human behavior involves synchronizing body movements with the musical rhythm through audio-motor interaction (Merchant et al., 2015; Patel and Iversen, 2014; Vuust et al., 2022; Zatorre et al., 2007). Yet not all forms of music induce dance equally. The musical quality and psychological construct associated with dance and the pleasurable wanting-to-move experience is called groove (Janata et al., 2012). The mere fact that humans spontaneously dance to specific types of musical stimuli speaks in favor of the dynamic and integrated nature of cognitive processes. In particular, it emphasizes the closed-loop nature of the action-perception cycle and exemplifies active sensing frameworks (see below; (Crapse and Sommer, 2008; Schroeder et al., 2010)). Investigation of the groove phenomenon shows that motor contributions to auditory perception involve temporal processing and arise when precise temporal expectations (or “priors”) are violated by sensory evidence (Vuust et al., 2022). In the context of music, these temporal violations (or “prediction errors”) are captured by the degree of syncopation – defined as the appearance of a beat on a metrically weak (unexpected) accent preceding a rest on a metrically strong (expected) accent. The experience of groove occurs during perception of recurring syncopated rhythmic patterns, with the relationship between the degree of syncopation and perceived groove being non-linear (Vuust and Witek, 2014; Zalta et al., 2023). This relation can be modelled with dynamical system approaches, or as the interaction between the degree of syncopation and the precision (or metrical certainty) of the internal model of temporal structure (Vuust et al., 2022; Zalta et al., 2023).

Temporal predictability optimizes motor processing

While the temporal predictability of musical rhythms induces spontaneous movement for pleasure, the temporal predictability of sensory input can be used in a more practical way to optimize behavior. For instance, going through the same traffic light every day builds an association between duration (the length of time for which the light stays red) and action (accelerating away once the light changes color). This association creates a temporal expectation (or “prior”) that allows you to predict the moment at which the light will turn green so that you can accelerate away more quickly. Experimentally, the behavioral benefits of temporal predictability have been extensively explored and documented. Studies repeatedly show that knowing when an event will happen improves both perceptual and motor processing of that event: temporally predictable events are perceived more easily and more quickly, they are better encoded into working and long-term memory, and are responded to more quickly (Nobre and van Ede, 2018, 2023). Yet the motor benefits of temporal predictability are not restricted to response speed. Several studies have examined the effects of temporal preparation on motor mechanisms by manipulating the length of the interval (or “foreperiod”, FP) between a warning cue and a target in a simple RT task. In the variable FP paradigm, the FP varies from one trial to another. As the conditional probability of target appearance gradually increases as the FP elapses, participants both respond more quickly (Niemi and Näätänen, 1981) and exert less force on the response button (Mattes and Ulrich, 1997; Jaśkowski and Verleger, 1993). In other words, temporal predictability speeds responses whilst simultaneously reducing the muscular effort needed to make these responses, suggesting that it might improve motor efficiency. Support for this hypothesis has come from neurophysiological studies of the fixed FP paradigm in which the FP is consistently short in one block but consistently long in another block. Since, according to Weber’s Law, temporal variance increases with the length of the interval, temporal estimates of short FPs are more precise than estimates of long ones, meaning that participants are better prepared in short FP blocks. Accordingly, RTs are faster in short FP blocks than long FP ones (Niemi and Näätänen, 1981). In addition to these performance benefits, the peripheral motor units that contract the muscle of the responding hand are better synchronized in short FP blocks than long ones (Hasbroucq et al, 1995) and activation of the primary motor cortex contralateral to the response hand is lower (Tandonnet et al, 2006). A strikingly similar pattern of findings was revealed by single unit recordings of the primary motor cortex in monkeys. Over several months of training on a fixed FP task, RTs to the target got steadily faster indicating that monkeys were learning to predict the time of target onset. In parallel, neural firing in primary motor cortex became tuned to the temporal structure of the task. At the predicted time of target onset, neural firing was better synchronized and the mean firing rate in the population of recorded neurons was lower overall (Kilavik et al, 2009). The performance benefits of temporal predictability might therefore be mediated by enhanced network efficiency: better synchronization and lower firing rates.

More recently, we’ve shown that human participants who learn to predict the onset time of a target within a single experimental session get progressively faster, and the muscular force used to make the response gets steadily smaller, again indicating improved motor efficiency (Thomas et al, 2019). In this study, participants performed a whole-body pointing task towards a response button that was just slightly out of reach. They responded to the presentation of a visual target that appeared after either a fixed FP in one session, or after a variable FP in another. During the pointing movement, electromyographic (EMG) recordings

of the tibialis anterior in the ankle allowed changes in activation of the muscle to be tracked over the course of the session (50 trials). When the target was presented after a fixed FP, RTs to the target got steadily faster and the EMG amplitude of tibialis activation got progressively lower. By contrast, when the time of target onset could not be predicted in the variable FP session there was no change in RT or EMG amplitude. Temporal predictability therefore optimized motor efficiency, both improving performance and reducing muscular effort. Notably, these muscular changes occurred even in muscles that were far from the primary response effector, indicating a distributed, whole-body motor effect (Thomas et al, 2019).

Temporal predictability not only optimizes motor activity related to limb movements, but also affects various types of oculomotor behavior. For instance, saccades (Dankner et al, 2017), microsaccades (Amit et al, 2019; Denison et al, 2019) and blinks (Amit et al, 2019; Abeles et al, 2020) are inhibited just prior to the presentation of temporally predictable, but not unpredictable, targets, even when no response to the target is required (Tal-Perry and YuvalGreenberg, 2021). Moreover, microsaccade inhibition occurs whether the temporal dynamics of stimulus processing are shaped implicitly by temporal probabilities (Amit et al, 2019) or explicitly by temporal cues (Denison et al, 2019; Tal-Perry and Yuval-Greenberg, 2020). These results demonstrate how temporal predictions influence basic motor mechanisms to optimize behavior. Blinks and microsaccades during stimulus presentation impair perception, therefore inhibiting such oculomotor activity at temporally probable or relevant moments in time would improve visual discrimination of any stimuli occurring at those times. Nonetheless, oculomotor inhibition has even been demonstrated during discrimination of tactile (Badde et al, 2020) or auditory targets (Abeles et al, 2020), with greater inhibition the more temporally predictable the targets are. Since oculomotor inhibition occurs even in the absence of a visual target, it might represent a generalized supramodal marker of temporal predictions. Such covert markers of temporal prediction, occurring before the target has even appeared, could complement more overt measures of temporal prediction, such as RTs, which are measurable only *after* the target has appeared. For instance, individuals with ADHD do not show the usual RT benefits of temporal predictability and also fail to show saccade inhibition prior to the predicted time, indicating that they have difficulty processing temporal regularities in stimulus presentation over and above any concomitant changes in performance (Dankner et al, 2017).

Temporal predictability can trigger impulsive behavior

Unfortunately, temporal predictability is not always beneficial for behavior. Although RTs to tactile targets in choice discrimination tasks are faster when targets appear after a fixed or highly probable FP (Lange and Röder, 2006; Badde et al, 2020), tactile sensitivity in a psychophysical task is impaired by the temporal regularity of target appearance (Kusnir et al, 2019). Kusnir et al (2019) found that when brief changes in auditory or tactile intensity were presented at fixed, rather than variable, intervals, detection thresholds were better for auditory stimuli but worse for tactile stimuli. The authors attributed this dissociation to the fact that, by contrast with visual and auditory perception, our perception of touch is often determined by the force of our own motor acts. Self-generated action induces sensory suppression mechanisms that cause the predicted sensations of our own motor acts (the “efference copy”) to be perceived as weaker than those imposed by external stimuli (e.g. Blakemore et al,

1999). By analogy, passive tactile stimuli occurring at predictable moments in time may be similarly subject to tactile suppression mechanisms, leading to reduced perceptual sensitivity.

Even within the visual modality, in which temporal predictability has typically been shown to benefit performance, it can be detrimental when stimulus characteristics trigger potentially competing responses. For instance, Correa et al (2010) showed that temporal predictability exacerbates the interfering effects of incompatible stimulus-response associations in classic response conflict paradigms, such as the flanker or Simon tasks. In the flanker task, participants make left or right response buttons according to the direction indicated by a central arrow. This arrow is flanked on either side by arrows whose direction either match (compatible) or not (incompatible) the direction of the central arrow. Typically, RTs are slower for targets with incompatible flankers due to the conflicting responses induced by the directions of the task-relevant central arrow and the flanking distractors. In the Simon task, left or right button presses are associated with a specific stimulus feature, such as color (press left for blue stimuli and right for red) or shape (press left for x and right for +). Crucially, the side of the screen on which stimuli are presented either matches (compatible) or not (incompatible) the response side indicated by the target. Again, RTs are slower for incompatible targets due to the response conflict induced by the task-relevant stimulus feature and the more salient, though task-irrelevant, target location. Correa et al (2010) adapted these classic paradigms by presenting stimuli at times that were either temporally probable (75%) or improbable (25%) within a given block, with the hypothesis that temporal predictability would mitigate the RT costs of response conflict. However, in both flanker and Simon tasks, RTs to incompatible stimuli were even slower when they appeared at expected, rather than unexpected, times (Correa et al, 2010). In other words, temporal predictability exacerbated the motor cost of response conflict (see also van Driel et al, 2015 for a complementary approach). Correa et al (2010) suggested that temporal predictability increased motor readiness to respond to both task-relevant and task-irrelevant features. As such, responses to compatible stimuli would accelerate due to the combined influence of the task-relevant and irrelevant features. By contrast, responses to incompatible stimuli would be both slower and more error-prone because the interfering influence of the task-irrelevant feature would counteract that of the task-relevant feature.

We have followed up this research in a series of studies in which temporal predictability in the Simon task was manipulated with temporal cues rather than stimulus probabilities. Specifically, a temporal cue predicted whether the subsequent target would occur after a short or a long interval whereas a neutral cue provided no predictive information, with the target equally likely to occur after the short or long delay (Figure 1a). Since short and long interval trials were intermixed within blocks, participants could use temporal cues to voluntarily orient their focus of temporal attention to different moments in time from one trial to the next. We first confirmed Correa et al's (2010) findings that the RT cost of incompatible targets was greater when they were temporally predictable. Second, we demonstrated that in the fastest section of the RT distribution, when participants are responding particularly quickly and making more errors to incompatible stimuli, these errors were even more frequent in the temporal cue condition than the neutral cue condition (Korolczuk et al, 2018). In other words, when the time of target appearance could be predicted in advance, it was harder to stop the automatic impulse to make a response with the hand associated to the more salient, but task-irrelevant, feature. This result indicates that temporal predictability induces a greater number of fast, impulsive errors and supports the hypothesis of increased response readiness.

Figure 1 about here please

Further support for this hypothesis came from EMG recordings of the response hands. EMG allowed us to detect small, sub-threshold “twitches” in the muscles of the *incorrect* response hand that occasionally occur before the response with the *correct* hand is given. These twitches, termed “partial errors”, are usually caught and corrected before becoming fully fledged supra-threshold errors (Burle et al., 2002; Servant et al., 2015). Nevertheless, the number of these covert partial errors provides a measure of susceptibility to automatic response capture by the task-irrelevant stimulus feature, independent of any subsequent correction (inhibition) processes. Korolczuk et al (2020) found that temporal cueing not only increased the number of overt impulsive errors, confirming prior results, but also increased the number of covert partial errors. Moreover, these partial errors were made more quickly when the target was temporally predictable. By contrast, temporal predictability did not affect the number of covert partial errors that were subsequently followed by a correct overt response. Taken together, this pattern of results indicates that participants quickly began to activate the wrong response hand but then corrected their mistake before it became an overt motor response. Very similar findings were reported by Menciloglu et al (2021) using a fixed FP flanker task, in which participants used a computer mouse to reach towards the left or right response side rather than simply pressing a left or right button. Analysis of reaching trajectories allowed covert response tendencies to be tracked. If flankers were incompatible with the direction indicated by the central arrow, trajectories initially curved towards the side indicated by the task-irrelevant flankers before then being adjusted back towards the correct response side. Temporal predictability exacerbated the effects of response conflict on reaching dynamics: trajectories to incompatible targets were even more curved towards the competing side when participants knew when the target was going to appear. Together, these studies demonstrate how careful analysis of movement parameters (EMG or reach trajectory) helps uncover the effects of temporal predictability on motor control more completely. Online inhibition of these automatic, yet covert, response impulses would never have been revealed by simply measuring mean RT. Instead, analyses of sub-threshold EMG activity or trajectory dynamics show that temporal predictability increases the urge to initiate premature, yet potentially erroneous, prepotent responses, which can nevertheless still be corrected before the final response is delivered.

Temporal predictability modulates motor activity not only during the execution of the motor response itself. We recently combined EMG with electroencephalography (EEG) to show that temporal predictability can modulate motor activity related to the resolution of response conflict before response execution has even begun. We recorded activity over left and right primary motor cortices, which were contralateral to either the correct or incorrect response hand in a temporally cued Simon task (Korolczuk et al, 2022). Simultaneous EMG recording allowed the onset of motor responses to be pinpointed with high temporal precision. We hypothesized that temporal predictability would improve RTs to compatible targets by increasing motor activation in the hemisphere contralateral to the correct hand and /or decreasing motor inhibition in the hemisphere contralateral to the incorrect hand. Results showed that, in fact, temporal predictability had no effect on activity in the motor cortex contralateral to the correct hand in this response conflict paradigm (Figure 1b, top). Instead, it differentially modulated inhibitory activity in the motor cortex contralateral to the *incorrect* response hand as a function of target compatibility (Figure 1b, bottom). When target features were compatible, temporal predictability increased motor inhibition in the hemisphere

controlling the incorrect response hand and performance improved. Conversely, when target features were incompatible, triggering two conflicting responses, temporal predictability decreased motor inhibition in the hemisphere controlling the incorrect hand, and impulsive responding increased. This neurophysiological dissociation explains both the performance benefits of temporal predictability for non-conflict stimuli and performance costs for conflict stimuli. These inhibitory effects occurred after the target had been presented but approximately 100ms before the EMG-defined onset of the motor response, indicating a clear effect of temporal predictability on motor planning rather than response execution.

The effects of temporal predictability on motor inhibition are further corroborated by the results of a temporally cued version of the Stop-Signal Task (Korolczuk et al., 2018). The Stop-Signal task is a visual choice RT task in which 25 % of trials contain an auditory stop signal, presented very soon after the target appears, signalling that participants should withhold their response to the target on that trial. Korolczuk et al (2018) adapted this paradigm by including temporal or neutral cues (similar to those shown in Figure 1a) at the beginning of each trial, which either predicted (temporal cue) or not (neutral cue) when the target would occur i.e. after a short or long interval. As expected, temporal (versus neutral) cues speeded RTs on the 75% of “go” trials that did not contain a stop signal. By contrast, when participants had to withhold their response in the “stop” trials, temporal cues *impaired* performance: it took participants longer to stop their response to the target when the time at which it would appear was entirely predictable. The complementary pattern of results demonstrates that temporal predictability facilitates motor responding to a target in go trials but makes it harder to inhibit the response in stop trials. In other words, temporal predictability lowers the response threshold, sometimes to detrimental effect.

Rhythmic movements enhance sensory processing

Temporal predictions not only guide motor control but can also facilitate sensory processing. Behavioral experiments demonstrate that anticipating the temporal occurrence of an upcoming event optimizes its processing by improving the quality of visual (Cravo et al., 2013; Doherty et al., 2005; Rohenkohl et al., 2012) or auditory (Jaramillo and Zador, 2011; Morillon et al., 2016; Wollman and Morillon, 2018) information. More naturalistic acoustic signals, such as speech and music, also exhibit reliable temporal regularities that can be used to generate temporal predictions (Ding et al., 2017). While the temporal structure of environmental signals has been mostly overlooked until now, recent results crucially reveal the unique role of the motor system in the analysis of perceptual temporal dynamics. One of the contributions of the motor cortex to sensory processing would be in the analysis of the slow temporal dynamics of the perceptual stream, likely providing a contextual temporal framework to parse sensory information, thereby improving the quality of perceptual processing. This contribution of motor areas is likely modality- and domain- general and would occur during perception of any sensory signal temporally structured with low-frequency dynamics. Accordingly, coupling action to temporally predictable sensory streams, such as auditory rhythms, enhances sensory processing even more. From early childhood (< 1 year), infants' movements influence their perception of auditory rhythms (Phillips-Silver and Trainor, 2005), suggesting that the contribution of the motor system to time perception is innate. Rhythmic action training helps children aged 5 years old to accurately reproduce a rhythmic sequence and, more interestingly, helps both 5- and 8-

year olds to discriminate the trained rhythm in a purely perceptual timing task (Monier et al., 2019). Moving in time to a rhythmic stimulus helps adults (Phillips-Silver and Trainor, 2007), especially non-musicians (Su and Pöppel, 2012; Zalta et al., 2020), find the beat in ambiguous rhythms and improves perceptual estimates of duration (Manning and Schutz, 2013, 2016). Even simply imagining rhythmic movement strengthens performance benefits of the temporal predictability of a stimulus stream (Fautrelle et al., 2015). The temporal information implicitly embedded within rhythmic movements therefore helps construct an explicit, independent, and flexible representation of duration that can be used to make accurate perceptual temporal discriminations.

In a set of studies, we investigated the influence of overt movements on the quality of auditory temporal attention (Morillon and Baillet, 2017; Morillon et al., 2014). We focused on the auditory modality because of its relative bottom-up disconnection from the motor system. Indeed, while bottom-up and top-down motor influences are contingent in most sensory modalities, audition is the exception since we cannot selectively move our ears. Hence, bottom-up auditory processing is remarkably divorced from movement, whereas movement can modulate auditory processing through top-down corollary discharge (/efference copy) signals (see below; Morillon et al., 2015; Schroeder et al., 2010). We measured the ability of human participants to extract relevant melodic information embedded in rhythmic streams that were interleaved with distractors, as in the cocktail-party effect (Cherry, 1953), where listeners must “tune in” to one conversation in a noisy scene. We used a perceptual decision-making task, to measure the effects of temporal attention over an extended time period. Participants were asked to categorize sequences of eight pure tones as being higher or lower pitched, on average, than a reference frequency. To drive rhythmic fluctuations in attention, the tones (targets) were delivered in phase with a reference beat, presented at the beginning of each trial, and in anti-phase with irrelevant yet physically indistinguishable tones (distractors). Hence, only the temporal dimension, namely an accurate internal representation of the beat, allowed participants to discriminate targets from distractors (see Figure 2a). Participants were instructed either to use their motor system overtly, by tapping in time with the reference beat, or to keep the rhythm covertly, in both cases as a way to optimize the allocation of temporal attention (predictions) in a purely internally driven fashion. Our findings showed that the active implication of the motor system improved the precision of temporal attention and the quality of sensory processing. In other words, moving in time to a periodic stimulus improves the temporal segmentation of auditory information and improves perceptual discrimination of non-temporal features (here, pitch) of stimuli occurring on the beat. Moreover, the motor-related improvement in auditory segmentation depended parametrically on the temporal predictions made by the motor system: the more rhythmic the auditory sequence and the better able participants were to tap rhythmically, the more they benefitted from overt motor rhythms to extract auditory information (Morillon et al., 2014). Our results therefore reinforce the idea that the motor system is intrinsically engaged in the analysis of temporal sequences (see below).

Figure 2 about here please

In a more recent study, we investigated the sampling capacities of periodic temporal attention during auditory or visual perception (Zalta et al., 2020). We developed a paradigm to behaviorally quantify the sampling capacities of periodic temporal attention during auditory and visual perception. Sequences of stimuli were presented on each trial, from 2 to ~20 s. Three reference stimuli defining the tempo (or beat frequency) of the isochronous event sequence preceded a mixture of on-beat and off-beat stimuli. Participants performed a beat discrimination task at the end of each trial, by deciding whether the last stimulus of the sequence, a deviant, was on or off beat. While on-beat stimuli reinforced the temporal structure, crucially, off-beat stimuli had a distracting influence. This interleaved delivery of sensory events forced participants to track the beat throughout the entire duration of the sequence while minimizing the interference of aperiodic events. This protocol thus ensured that their attentional focus was temporally modulated over an extended time period. The density of distractors (i.e., number of distractors per beat) was adjusted for each participant prior to the experiment to reach threshold performance for a 2 Hz beat-frequency. The quality of temporal attention was estimated for different beat frequencies, ranging from ~0.5 Hz to ~4 Hz across conditions, to span most of the range of discernible tempi (Fraisse, 1948; McAuley, 2010; Moelants, 2002; Repp and Su, 2013; Woodrow, 1951). In each modality, we first investigated temporal attention during passive perception — i.e., without overt motor involvement — and then quantified in another set of experiments the motor contribution to temporal attention. Through six interrelated behavioural experiments, we revealed the existence of a limited sampling capacity of temporal attention which, importantly, was sensory-specific (~1.4 Hz in audition, ~0.7 Hz in vision). In addition, we demonstrated that the motor contribution to temporal attention was also sensory-specific and derives from the compatibility of temporal dynamics underlying motor and sensory-specific attentional processes. Indeed, we showed that the motor contribution to temporal attention scales with motor rhythmic precision, which is maximal at ~1.5-2 Hz (Fraisse, 1948; Woodrow, 1951). Moreover, this effect crucially depends on the temporal simultaneity of motor acts relative to the beat (Morillon et al., 2014; Zalta et al., 2020). Finally, in line with previous models of beat perception and temporal attention processes (Jones, 1976; Large and Jones, 1999; Large et al., 2015), we show that our results are reproduced by a simple dynamical model involving three coupled oscillators. While the optimal sampling rate of temporal attention is directly reflected in the natural frequency of the (auditory or visual) attentional oscillator, the quality of the motor modulation crucially depends on the time-delay in the coupling between the stimulus and the motor oscillator. These results suggest that specific rhythmic sampling rates emerge from the specific configuration of large-scale neural networks encompassing sensory regions, in addition to attentional and motor areas (Donner and Siegel, 2011; Siegel et al., 2012). Future models and experiments need to further investigate how these multiple neural structures –devoted to specific algorithmic processes and having specific temporal constraints– are dynamically coordinated to subservise or facilitate perceptual processing.

Active sensing as a fundamental mechanism of perception

Active sensing describes the fact that perception is intrinsically shaped by motor dynamics (Morillon et al., 2015; Schroeder et al., 2010). Indeed, our sensory organs are not passive

receptacles for stimulation but are part of an action-perception closed-loop system (Ahissar and Assa, 2016). Sensory inputs are acquired through overt motor sampling behaviors, such as hand or eye movements in primates and whisking or sniffing in rodents. Consequently, motor acts and associated neural dynamics temporally structure the activity of sensory cortices and, consequently, the processing of incoming sensory inputs.

Attention is an essential component of the process, helping to impose a motor sampling pattern on the relevant sensory stream (visual, tactile...). In addition to driving activity in sensory areas by volleys of ascending input (through movement of the sensory organ), there is top-down (corollary discharge and/or attentional) modulation, all yoked to movement (Schroeder et al., 2010). The corollary discharge signals provided by motor areas to sensory systems convey system-specific information content (spatial, spectral, etc.) as well as contextual temporal information (i.e., the underlying temporal framework; (Crapse and Sommer, 2008)). Thus, perceptual information is sampled according to the rhythms of overt action, but also the rhythms of covert motor and/or attentional dynamics. As illustrated by whisking and sniffing in rodents and saccadic sampling during free viewing in primates, motor-driven information sampling routines follow temporally periodic patterns (McAuley et al., 1999; Wachowiak, 2011).

Covert attentional sampling is a form of active sensing that takes over where overt motoric sampling is not at play. In the auditory domain a form of overt active sensing is lacking, as bottom-up auditory processing is remarkably divorced from movement (Morillon et al., 2015; Schroeder et al., 2010). However, a *covert* form of active sensing is present, with oscillatory influences from motor cortex modulating activity in auditory regions during perception (Arnal, 2012; Merchant et al., 2015; Morillon and Schroeder, 2015; Morillon et al., 2015; Patel and Iversen, 2014). When perceiving several rhythmic sensory streams simultaneously (e.g. one conversation at a cocktail party), dynamic attentional filtering facilitates the processing of one task-relevant stream at the expense of all others. This occurs whether attention is selecting between modalities (Lakatos et al., 2009), within a modality (Lakatos et al., 2013) or integrating across modalities (Zion Golumbic et al., 2013). Motor system neural dynamics are implicated in both covert-attentional and overt-motoric sampling of sensory input. Motor and premotor cortices consistently emerge as the most active regions in studies of rhythmic (Morillon et al., 2015) or temporally cued (Coull and Nobre, 1998; Davranche et al, 2011; Coull et al, 2013) attentional selection. According to the premotor theory of attention, covert shifts in spatial attention are governed by the same circuitry that controls overt shifts in eye position (Rizzolatti et al., 1987). Although one can argue specific tenets of the theory (Smith and Schenk, 2012), it clearly underscores a fundamental relationship between motor systems and active/attentive sensory processing. This relationship comes to the fore when the temporal predictability of sensory input is used to optimize behavior (traffic light, musical beat, etc.). Accordingly, it has been proposed that time perception relies on the neural recycling of action circuits and is implemented by internal, non-conscious 'simulation' of movements in most ecological situations (Schubotz, 2007; Coull and Droit-Volet, 2018; Arnal, 2012; Patel and Iversen, 2014; De Kock et al., 2021; Robbe, 2022). This idea mirrors the central proposition of the premotor theory of attention in which the transmission of temporal information from motor to sensory

regions could be implemented through corollary discharge signals (Crapse and Sommer, 2008; Nobre and van Ede, 2018; Khalilian-Gourtani et al., 2022).

Motor cortex rhythms as intrinsic temporal constraints of perception

Cortical rhythms correspond to the periodic shifting of neuronal populations between states of high and low excitability, which coordinates neural communication (Wang, 2010). In the motor cortex, most of the existing data point to beta oscillations (~12-30 Hz) as a predominant and specific rhythm during rest and to coordinate information transfer in action planning and execution. However, using finer-grained spectral analysis methods to analyze recordings from the motor cortex reveals a much more complex picture (Morillon et al., 2019). In humans for example, ongoing oscillatory activity of the primary motor cortex is characterized by consistent spectral peaks, principally in the delta (0.5-4 Hz) and beta frequency ranges (Keitel and Gross, 2016). Interestingly, these oscillatory rhythms are hierarchically structured in time (Lakatos et al., 2005). For example, a functionally relevant delta-beta phase-amplitude coupling has been shown in the motor cortex during auditory (Arnal et al., 2015; Keitel et al., 2018; Morillon and Baillet, 2017) and visual (Saleh et al., 2010) perception. This specific spectro-spatial pattern of activity represents temporal information and is directly related to behavioral performance in tasks involving perceptual temporal processing. Increases in the sensory quality of information presented at predictable moments in time (Nobre and van Ede, 2018) are reflected in the reorganization of low-frequency neural oscillations, which temporally modulates the excitability of task-relevant neural populations, and thus acts as an instrument of sensory selection (Schroeder and Lakatos, 2009). This neural reorganization is visible in sensory cortices, but also in higher-order associative attentional and motor regions (Besle et al., 2011).

Multiple findings converge to support the relevance of intrinsic delta oscillations, at the functional and behavioral levels, whenever rhythmicity, i.e. temporal predictability, is observed. For instance, walking, a most basic motor act, is fundamentally rhythmic and operates within the delta range (2 Hz; (MacDougall and Moore, 2005)). Strikingly, this mirrors spontaneous oscillatory activity in the motor cortex (~2 Hz). Spontaneous rhythmic motor behaviors such as finger tapping also function at a preferred tempo of ~1.5-2 Hz, and motor tapping has an optimal temporal precision at around ~0.8-2.5 Hz (Fraisse, 1948). Moreover, during production of speech, an extremely complex motor behavior, the coordination of articulatory movements is encoded in kinematic trajectories characterized by delta oscillatory dynamics (Chartier et al., 2018). Even during reaching, a non-periodic motor behavior, motor trajectories are encoded in patterns of neural dynamics that oscillate at around 1-2 Hz (Churchland et al., 2012). Delta dynamics in motor areas also anticipate the timing of informative cues in motor planning (Saleh et al., 2010; Cadena-Valencia et al., 2018) and are tuned to temporally predictable targets requiring resolution of response conflict in the Simon task (Koroleczuk et al, 2022; Figure 1c). Delta oscillatory dynamics are also argued to be responsible for cognitive phenomena such as attentional blink, inhibition of return and the psychological refractory period (Schroeder and Lakatos, 2009; Wyart et al., 2012). Overall, delta oscillations shape the dynamics of neural activity in the motor cortex and of motor behaviors and appear to impose a temporal framework that both enables and constrains the

sampling of perceptual information. In other words, a proactive simulation process is effected by delta oscillations which constrain the speed at which temporal processing occurs.

Temporal predictions have consistently been shown to originate at least in part in motor cortex (Morillon and Baillet, 2017) and regions associated with motor planning, such as left inferior parietal cortex (Coull, 2014; Naghibi et al, 2023). In a magnetoencephalography (MEG) experiment, we asked human participants to perform auditory categorizations of sequences of pure tones, composed of an interleaved delivery of targets and distractors (Morillon et al., 2014). This paradigm mirrors the cocktail-party effect (Cherry, 1953), with the “noisy” signal occurring at a rate of ~3 Hz while temporal attention is guided to temporally predictable targets at ~1.5 Hz (see Figure 2 and above). We observed that while the acoustic signal drives cortical dynamics in and around auditory regions, the left sensorimotor cortex encodes the temporal predictions that allow for precise temporal anticipation of forthcoming sensory inputs at 1.5 Hz. Moreover, this encoding is associated with bursts of beta (18–24 Hz) neural oscillations that are directed toward auditory regions. When participants were instructed to use their motor system overtly, by pressing a button in time with the reference beat (similar to (Morillon et al., 2014)) the quality of temporal predictions increased and enhanced auditory task performance even more. These behavioral changes were associated with increased signaling of temporal predictions in right-lateralized frontoparietal associative regions, involved in melodic processing and auditory memory for pitch (Zatorre et al., 1994). This study points at a covert form of auditory active sensing and emphasizes the fundamental role of left-lateralized motor brain areas and actual motor behavior in sensory processing. Attentional modulation of auditory information thus depends on the downward propagation of such temporal information represented in delta-beta phase-amplitude coupled oscillations in motor cortex (Arnal et al., 2015; Morillon and Baillet, 2017; Saleh et al., 2010).

Conclusion

Temporal regularities in sensory input can be automatically or voluntarily extracted and exploited to optimize both perceptual processing and motor behavior. Moreover, the influence between the motor system and timing is mutual. The temporal predictability of sensory input affects a wide variety of motor behaviors, including speed, force and impulsivity. Reciprocally, motor behavior hones temporal precision and leads to a more robust representation of time. By boosting the precision of the temporal representation through movement, temporal predictions become more accurate and the motor and sensory processing of events occurring at predicted moments in time is heightened. While enhanced sensory processing of predictable events will generally serve to optimize behavior, it could induce maladaptive impulsive behavior by triggering responses to salient but irrelevant events. Importantly, faster responses to temporally predictable events will further tighten the coupling between action and time, which could then feed back within a closed-loop system to enhance the temporal precision of predictions even more, and so continually fine-tune sensorimotor processing. The intertwined relationship between motor activity and temporal information processing may be mediated by delta-range oscillatory activity in the motor cortex, such that oscillatory dynamics become tuned to the temporal predictability of sensory input, thereby shaping the sampling of perceptual

information. More generally, this outline is directly compatible with the active sensing framework, which attributes the motor system with a fundamental role in perception.

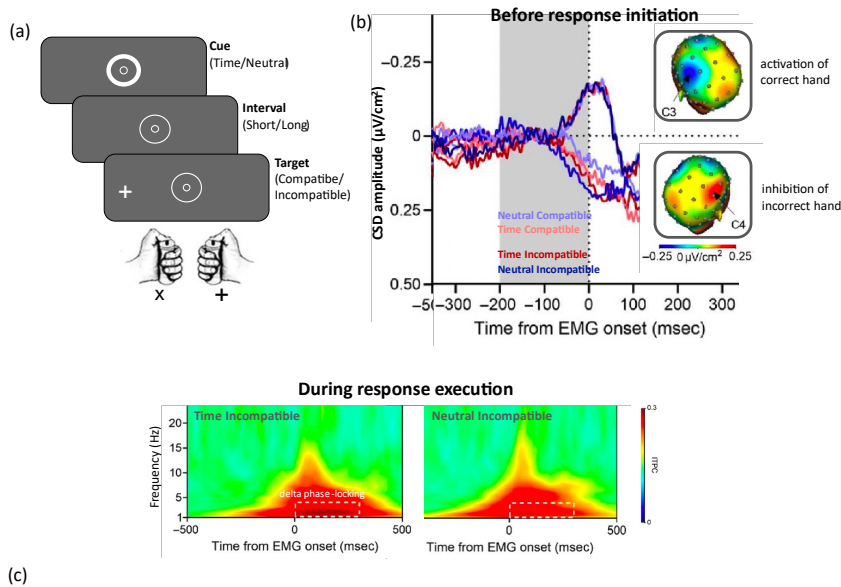


Figure 1. Temporal predictions modulate motor cortex activity during response conflict

- (a) Temporal Simon task: Time cues indicated whether the target would occur after a short (small circle) or long (large circle) interval. Neutral cues (both circles) gave no information about target onset. Target shape was associated with left/right hand responses (counterbalanced across participants). Target location could be either compatible or incompatible with the correct hand response. In this example, the + appears on the left but should be responded to with the right hand and so is an “incompatible” target type. If it had appeared on the right of the screen, it would have been a “compatible” target.
- (b) After target presentation, but before initiation of the response (grey square), there was stronger inhibition (i.e. steeper slopes) of activity measured over the primary motor cortex contralateral to the *incorrect* response hand for temporally predictable (compared to neutral) *compatible* targets, but less inhibition for temporally predictable (compared to neutral) *incompatible* targets. By contrast, temporal predictability had no effect on motor cortex activity contralateral to the *correct* response hand prior to response initiation.
- (c) During response execution, delta phase locking measured over the primary motor cortex contralateral to the correct response hand was stronger for incompatible than compatible targets (not shown) and was stronger still when incompatible targets were temporally predictable. *From Korolczuk et al., 2022.*

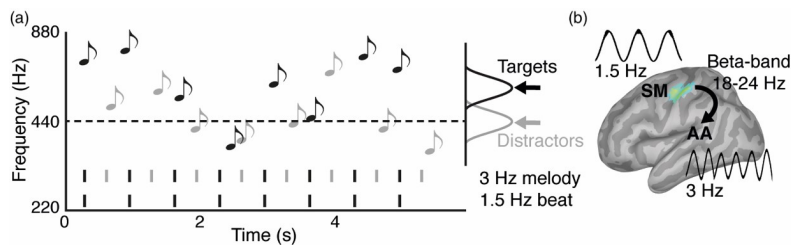


Figure 2. Temporal Predictions Mediated by Delta-Beta Coupled Oscillations.

- (a) Dynamic selective attention paradigm. Quasi-rhythmic sequences of tones were presented binaurally on each trial. Four reference tones (not shown) preceded an alternation of eight target and eight distractor tones of variable frequencies. Targets occurred in phase with the preceding references, whereas distractors occurred in antiphase. Participants had to decide whether the mean frequency of targets was higher or lower than the reference frequency. While auditory input occurs at 3 Hz (melody), participants temporally modulate their attention at 1.5 Hz (beat).
- (b) In this design, neural activity dedicated to stimulus processing or temporal prediction is hence dissociable based on its temporal dynamics (3 Hz vs. 1.5 Hz, respectively). While auditory association cortex (AA) tracked stimulus dynamics (3 Hz; not shown), temporal predictions were encoded in the left sensorimotor cortex (SM) in delta-beta phase-amplitude coupled (1.5 – 18-24 Hz) oscillations, functionally directed toward auditory regions to modulate the 3 Hz auditory input. *From Morillon and Baillet, 2017.*

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