# The common rhythm of action and perception

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## Abstract

Research in the last decade has undermined the idea of perception as a continuous process, providing strong empirical support for its rhythmic modulation. More recently, it has been revealed that the ongoing motor processes influence the rhythmic sampling of sensory information. In this review, we will focus on a growing body of evidence suggesting that oscillation-based mechanisms may structure the dynamic interplay between the motor and sensory system and provide a unified temporal frame for their effective coordination. We will describe neurophysiological data, primarily collected in animals, showing phase-locking of neuronal oscillations to the onset of (eye) movements. These data are complemented by novel evidence in humans which demonstrate the behavioral relevance of these oscillatory modulations and their domain-general nature. Finally, we will discuss the possible implications of these modulations for action-perception coupling mechanisms.

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## Movement-locked synchronization of neuronal oscillations

Research in the last decade has provided a solid empirical basis for the longstanding postulate that perception may not be continuous, but rather modulated in a rhythmic fashion (Harter, 1967; VanRullen, 2016; Varela et al., 1981). Cyclic fluctuations of neuronal excitability inherently structure the way the brain samples and processes the external inputs over time. This rhythmic neural machinery does not act as a passive sensory filter but flexibly tunes sensory processing in space and time to optimize it. The ongoing dynamics in brain oscillatory states is subjected to both bottom-up influences as well as top-down control. For example, oscillations can be synchronized, or phase-reset, by exogenous cues. This unmasks cue-locked rhythmicity in behavioral performance (e.g. detection and reaction times), with visual sampling alternating across attended locations and objects (Drewes et al., 2015; Fiebelkorn et al., 2018; Helfrich et al., 2018; Holcombe and Chen, 2013; Huang et al., 2015; Jia et al., 2017; Landau et al., 2015; Landau and Fries, 2012; Song et al., 2014). On the other hand, in the presence of temporally predictable sensory stimuli, brain oscillations actively adjust to align in time the high (low) excitability states with the expected events, leading to sensory enhancement (suppression) of relevant (irrelevant) stimuli and consequent behavioral benefits (Bonnefond and Jensen, 2012; Cravo et al., 2011; Lakatos et al., 2009; Morillon et al., 2015; Samaha et al., 2015; Schroeder and Lakatos, 2009; Stefanics et al., 2010).

Natural stimuli often contain temporal regularities, and our brain exploits them predictively via ongoing oscillatory phase alignment (e.g. see Besle et al., 2011; Lakatos et al., 2008; Morillon and Baillet, 2017; Saleh et al., 2010; Vander Ghinst et al., 2016; Zoefel, 2018). However, the temporal structure of the input arriving to our sensory organs is also shaped by our own movement. We actively collect, rather than passively register sensory information and we do so by constantly moving our receptors (Gibson, 1962). The visual function, which is tightly coupled with the incessant movement of the eyes, exemplifies the notion of *active sensing*.

That movement participates strongly to the sensory function is mostly evident in ‘exploratory’ behaviors – i.e., motor actions aimed at gathering sensory information – some of which are peculiar to the animal kingdom, such as sniffing and whisking. Intriguingly, these behaviors often display a rhythmic component. (Micro)saccadic eye movements, for example, are naturally performed at a rate of ~2-3 Hz (Rucci et al., 2018). The analogy between the overt rhythmicity of motor behavior and the covert rhythmicity of attentional sampling is appealing and some authors have suggested that they may rely on similar neuronal mechanisms

(Helfrich et al., 2018; Schroeder et al., 2010). Motor-related signals (e.g. corollary discharge) are available before the actual execution of a movement and may thus serve as endogenous predictive cues, to inform the sensory systems about the upcoming inputs. Traditionally, these anticipatory signals have been conceived instrumental to counteract the disruptive side-effects of movement on perception (Crapse and Sommer, 2008). For example, it is well known that they allow to filter out spurious self-generated signals by selective sensory suppression, and may participate to the mechanism mediating perceptual stability by updating and remapping spatial information across movements (Binda and Morrone, 2018; Burr and Morrone, 2011; Diamond et al., 2000; Medendorp, 2011; Ross et al., 2001). A corollary discharge signal may also operate a momentary boost of perceptual sensitivity to optimize processing of the new sensory inflow brought about by the movement itself (Melloni et al., 2009; Schroeder et al., 2010). This perceptual enhancement\suppression, similarly to that of attentional origin but time-locked to movement onset, might be achieved through the active modulation of neuronal oscillations.

Growing electrophysiological evidence, mostly deriving from monkey studies, shows that eye movements are accompanied by complex changes in oscillatory activity. These modulations affect multiple brain sites, including low and higher order visual areas (V1, V2, V4, superior temporal sulcus) as well as memory-related structures (e.g. hippocampus), and involve a wide range of frequencies (Bartlett et al., 2011; Bosman et al., 2009; Brunet et al., 2015; Hoffman et al., 2013; Ito et al., 2011; Jutras et al., 2013; Lowet et al., 2018, 2016; Neupane et al., 2017; Rajkai et al., 2008; Staudigl et al., 2017). The majority of these studies analyze the immediate post-fixational epoch, showing a phase-reset of low-frequency (delta\theta\alpha) oscillations, high-frequency (gamma) power modulations and an increase in spike-field coherence. However, these effects may not be caused by the movement itself but by the sensory consequences of the movement, such as the image refresh associated with the eye movement. Only few evidence points to a direct involvement of motor signals, like the demonstration of persistent oscillatory modulations when the eyes move on a homogenous screen (Ito et al., 2011) or in complete darkness (Rajkai et al., 2008). Yet, the relative contribution of motor- and sensory-driven signals is difficult to disentangle in many cases, especially when the frequency of the neuronal rhythm undergoing phase-modulations matches closely the saccadic rate. In this case, the periodically-evoked transients could easily be mistaken for ongoing oscillations (Deouell, 2016). In support of the motor-driven account, one early study, recording local field potentials (LFPs) in monkeys engaged in free-viewing of natural images, reported that alpha-beta oscillatory phases were more strongly locked to the onset of saccades compared to fixations (Ito et al., 2011). However, as for the majority of the studies (Bartlett et al., 2011; Hoffman et al., 2013; Jutras et al., 2013; Rajkai et al., 2008), phase concentration was confined only to the post-movement epoch. One exception to this finding is provided by a recently published study by Staudigl and colleagues (2017) who collected both intracranial and magnetoencephalography (MEG) data in humans during free exploration and memorization of visual images. The two datasets consistently show that alpha oscillations in visual and memory-related structures are phase-locked to saccade onset already 250 ms prior to the (self-initiated) movement. More interestingly, alpha phase-locking to saccades was stronger during visual scan of items that were subsequently remembered as opposed to forgotten, suggesting its functional relevance for the encoding, not just the sampling, of visual information (Staudigl et al., 2017).

The possibility that phase-alignment of slow rhythms could precede, and actually predict movement onset, has been also put forward by Bosman and colleagues (2009) for micro-saccades, although conclusive empirical proof is still lacking. The microsaccadic delta\theta-band rhythm (~2-4 Hz) periodically shapes local and interareal gamma-band synchronization in early visual areas (Lowet et al., 2018, 2016), indicating that it may have a fundamental role in regulating the information flow across the visual circuitry.

As outlined above, modulations of oscillatory activity at the time of eye movements are being increasingly documented by the rapid accumulation of data coming from electrophysiological recordings in animals. These studies, however, can hardly offer evidence of whether these modulations do actually bear any relevance for perception. More recent works, mostly behavioral but also neurophysiological, specifically address this issue in humans and show that movement-locked oscillations are indeed perceptually-relevant, anticipatory and, most importantly, not an exclusive property of the oculomotor system.

## Neuronal oscillations synchronize perception and action

In a series of studies, participants have been asked to perform a dual task: they had to execute a self-paced movement and, at the same time, to discriminate\detect a near-threshold visual stimulus which was briefly flashed at unpredictable times relative to movement performance. By using a time-resolved approach, visual perception was probed over a long time-window surrounding movement execution, allowing to reveal possible oscillatory traces in perceptual performance already during the motor planning phase (see figure 1).

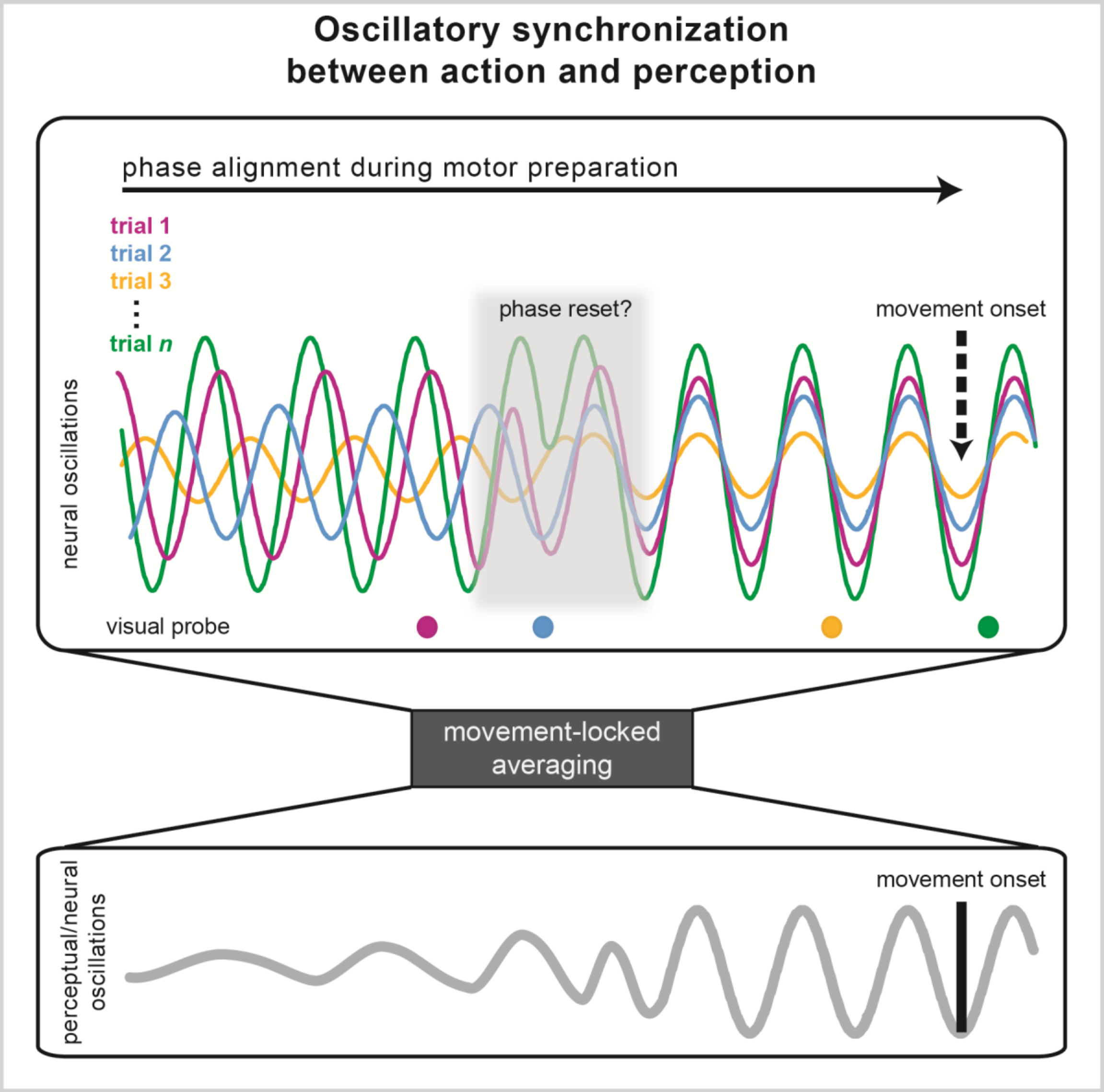


Figure 1. Schematic representation of the neuronal oscillatory modulations underlying the movement-locked fluctuations in visual performance and the main behavioral paradigm used to investigate this phenomenon. The colored lines show a cartoon of the ongoing delta/theta-band oscillatory activity during the pre-movement epoch in example trials. Movement onset (black arrow) occurs at a systematic phase (in this example the trough) of the ongoing rhythmic activity, revealing oscillatory phase-alignment to the (future) movement onset (see Tomassini et al., 2017).

Alternatively, movement-locking of delta/theta phases may be due to phase-resetting by an endogenous, movement-related, signal (e.g. corollary discharge) which is generated during motor preparation at a systematic moment in time before movement onset (grey shaded area). In each trial, a visual probe (colored dot) is presented at a random time (hence, at a random phase) both before and after movement onset. Movement-locked temporal averaging of the visual performance for the presented probes yields an oscillatory pattern (grey line; see Tomassini et al., 2015, 2017; Benedetto et al., 2016, 2017), reflecting 1) the influence of the ongoing phase on visual performance and 2) the consistent alignment of the ongoing phase to movement onset.

Benedetto and Morrone (2017) had participants performing continuous, slowly-paced, saccades (~1 saccade every 3 s) between two fixed targets, and probed visual contrast discrimination in-between movements. They found delta-band oscillations (~2-3 Hz) in visual performance which are time-locked to saccade onset, beginning ~1 s before and continuing up to 1 s after it (see figure 2). This unveiled an ongoing perceptual rhythm that clearly outlasts the short-lived neuronal modulations observed in the monkey electrophysiological recordings. Given the long inter-saccade interval (~ 3 s), the authors can also firmly exclude that the pre-movement rhythmicity reflects post-movement modulation due to the preceding saccade. This adds compelling evidence to the neurophysiological literature, by suggesting that eye movements are effectively coupled to an ongoing visual delta rhythm. Interestingly, saccadic visual suppression and post-fixational enhancement are embedded within the perceptual oscillation – i.e., they are both part of its phasic modulations – opening the possibility that the ongoing oscillation determines the time of the transient phenomena (Benedetto and Morrone, 2017). Nonetheless, they report that the rhythmic modulation in visual perception slightly changes its dominant frequency from the pre- (~3 Hz) to the post-saccadic (~2 Hz) epoch, indicating that saccade execution may introduce a discontinuity in the oscillatory dynamics (figure 2).

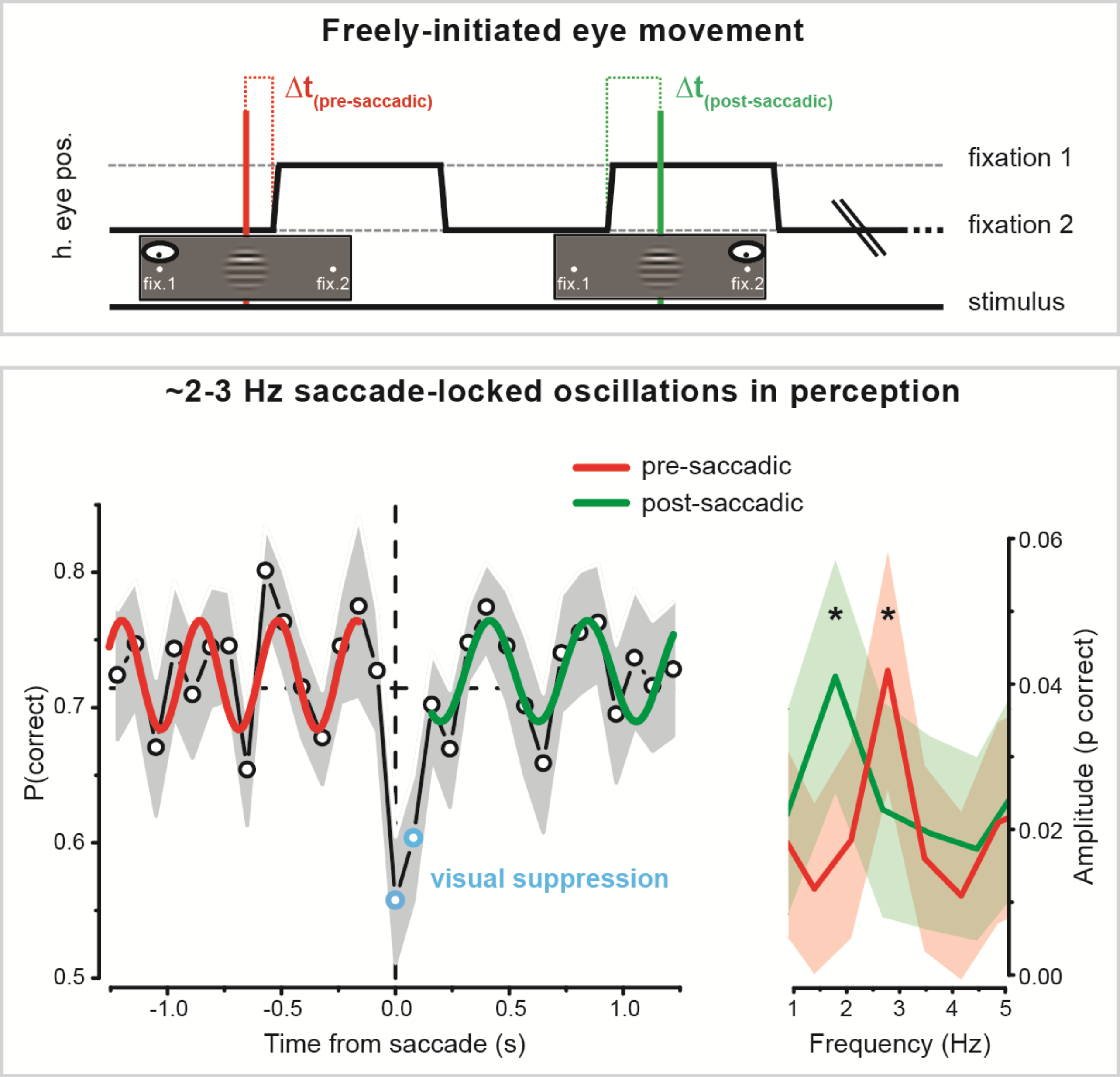


Figure 2. Box on top, experimental procedure from Benedetto and Morrone, 2017. Participants performed saccades at their own pace to stationary saccadic targets (fixation 1 and fixation 2). At random delays from the saccadic onset (Δt), a brief Gabor stimulus with a contrast increment in its upper or lower side was presented and participants reported the location of the increment. Box on bottom: left panel, Pre-saccadic and post-saccadic contrast discrimination performance as a function of time from saccadic onset. The gray area represents ±1 SEM from bootstrapping; thick lines

represent the best sinusoidal fit to the data for pre-saccadic responses (red, ~ 3 Hz) and for post-saccadic responses (green, ~2 Hz). Blue dots indicate the moment of maximal visual suppression caused by the execution of the saccade (saccadic suppression). Dashed vertical and horizontal lines indicate saccadic onset (time zero) and the median probability of correct response, respectively. Right panel, FFT mean amplitude spectra ±1 SEM for pre-saccadic responses (red) and post-saccadic responses (green), showing a significant peak at around 3 and 2 Hz, respectively. Asterisks indicate significance (0.05 > * > 0.01).

In a similar experiment, Hogendoorn et al. (2016) suggested instead that saccades do not reset the phase of visual oscillations: the pre-saccadic phase (and frequency) is in fact preserved after the eye movement, although for a shorter time compared to what reported by Benedetto et al. 2017 (~500 ms compared to ~1 s). The across-movement phase preservation leads Hogendoorn to speculate that eye movements, rather than playing an active role, may be themselves constrained by the phase of an ongoing rhythm, presumably of attentional origin (Hogendoorn, 2016). Both studies report saccade-related behavioral rhythmicity to be confined within the delta-band (2-4 Hz; see also Wutz et al., 2016 for consistent results, further discussed below). Higher-frequency (alpha\beta) oscillations of behavioral performance (visual reaction times) after a micro-saccadic movement have also been reported recently (Bellet et al., 2017). Interestingly, this alpha\beta oscillatory period that follows a micro-saccade, is further modulated by a slower oscillatory dynamic, alternating between visual hemifields at a rate of ~2.5 Hz, with the initial hemifield preference being coherent with the direction of the micro-saccadic movement. This alternate hemifield-switching recalls the anti-phasic fluctuation of spatial attention between different visual locations and objects (Fiebelkorn et al., 2013, 2018; Helfrich et al., 2018; Jia et al., 2017; Landau and Fries, 2012; Re et al., 2019). Recent monkey (Fiebelkorn et al., 2018) and human intracranial (Helfrich et al., 2018) data provide converging evidence that the rhythmic sampling of visual spatial locations is shaped by multiplexed oscillations across the fronto-parietal network, with higher-frequencies modulations being coupled to a lower, theta-band, neuronal rhythm. Altogether, this evidence points back to the long-debated link between attention and eye movements (Rizzolatti et al., 1987; Smith and Schenk, 2012) and raises the question of whether the saccadic initiation might actually be dictated by a covert attentional rhythm (Helfrich, 2018; Helfrich et al., 2018) , as suggested also by Hogendoorn (2016). More recently, Fiebelkorn and Kastner (2019) have proposed a model that aims at reconciling attention-based sensory sampling and eye movements control within a unified view. According to their proposal, two opposite states would alternate at a theta rhythm (Fiebelkorn and Kastner, 2019). A given phase of this theta rhythm would be associated with increased perceptual sensitivity (at the attended location) and concomitant motor suppression. As shown by the same authors (Fiebelkorn et al., 2018; Helfrich et al., 2018), this theta phase is coupled, at the behavioral level, with improved perceptual performance and, at the neural level, with high gamma power in parietal (LIP) /sensory areas and high beta power in motor-related (FEF) areas which index activity enhancement and suppression, respectively. The opposite theta phase would instead promote eye movements initiation and, at the same time, dampen sensory activity. Consistently, motor areas are released from beta-band suppression, while sensory areas are inhibited by alpha-band synchronization which could explain the decline in perceptual performance (Fiebelkorn et al., 2019, 2018). Within this model, sensory (sampling) and motor (exploratory eye movements) processes would be boosted at opposite phases of a common theta rhythm. This provides a possible explanation for the oscillations in human visual sensitivity in synchrony with saccadic eye movements onset described above (Benedetto and Morrone, 2017; Hogendoorn, 2016; Wutz et al., 2016).

Remarkably, oscillations in visual perception are not solely observed with movements of the oculomotor effector which, by imposing a displacement of the visual receptor (the retina), is by necessity both anatomically and functionally integrated with the visual system. Tomassini et al. (2015) asked participants to perform a (self-initiated) reaching movement with the right hand while monitoring two different spatial locations for the appearance of an unpredictable, low-contrast, visual target. Visual performance for both locations shows rhythmic, theta-band (3-7 Hz), periodicity that is time-locked to the hand movement. Like for saccades (Benedetto and Morrone, 2017), the observed action-locked perceptual rhythmicity emerges long before movement onset, suggesting an automatic coupling between visual processing and motor planning (Tomassini et al., 2015). In a follow-up electroencephalography (EEG) experiment, Tomassini and colleagues (2017) reveal the neurophysiological underpinnings of this coupling, showing that action planning is accompanied by an endogenous phase adjustment of perceptually-relevant neuronal oscillations (see figure 3). The authors found evidence of two distinct epochs in which theta (~4 Hz) phases are both predictive of visual perception (for later presented stimuli) and consistently aligned to the (future) hand movement: an early epoch, around 1.5 s before motor execution, and a later epoch, starting at 0.5 s and peaking at movement onset (see figure 3). Despite sharing the same spectral specificity, these two *visuo-motor* rhythms have different topographies (fronto-central and occipito-parietal in the early and late epoch, respectively) and, most importantly, they have independent predictive power for perception, suggesting that they might reflect two distinct processes which are initiated at different times during movement preparation (Tomassini et al., 2017). This depicts a more complex picture compared to what previously provided by the purely behavioral studies: multiple oscillatory signals are coupled to both motor and visual performance with varying temporal dynamics and spatial distribution, and they might therefore play distinct sensorimotor functions.

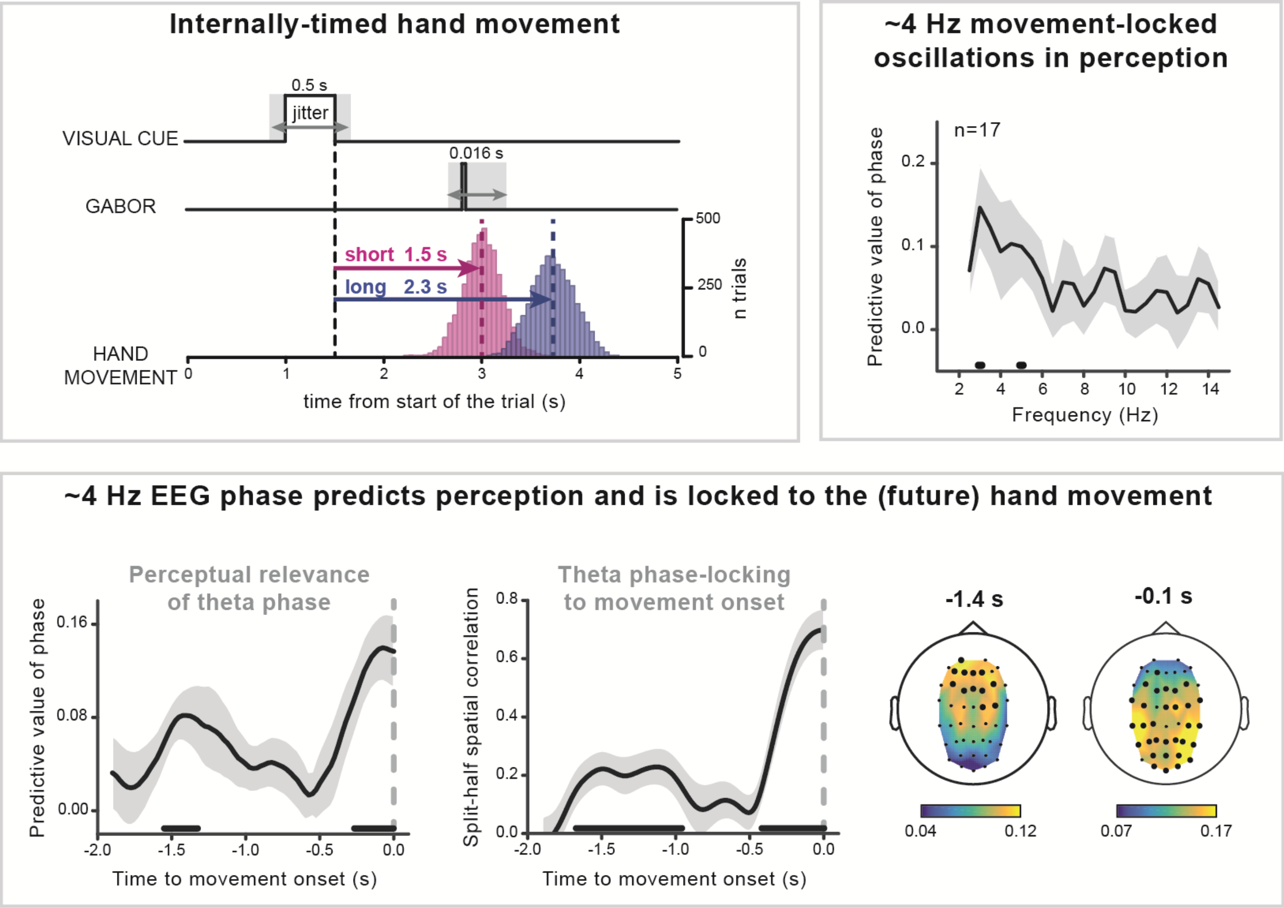


Figure 3. Box on top-left, timeline of the trial from Tomassini et al., 2017. A visual cue (change in color of the fixation cross) is shown after a variable delay from the start of the trial and indicates whether participants

have to wait for a short (1.5 s) or a long (2.3 s) time interval before executing the hand movement (isometric contraction). The visual cue offset marks the start of the time interval that participants have to wait before executing the movement. Bar histograms show the distribution of movement onset times for the short (pink) and long (blue) time intervals. The dashed vertical lines indicate the mean onset times (short: 1.5 ± 0.2 s; long: 2.22 ± 0.24 s; mean ± s.d.). At random times between –0.35 and +0.25 s relative to the instructed movement time, a near-threshold contrast Gabor tilted 45 deg clockwise or counterclockwise is briefly flashed for 16 ms. Box on top-right, predictive value of the phase of sinusoidal (basis) functions for perceptual performance (time-locked to movement onset). The gray-shaded area represents the jackknife standard error. The black horizontal bars indicate the significant frequencies ($p<0.05$). Box on bottom: left, predictive value of the 4 Hz theta (neuronal) phase for perception as a function of the time where the phase was estimated relative to movement onset. The gray-shaded area represents the jackknife standard error. Center, time course of theta phase-locking to movement onset (estimated by means of a measure of phase reliability; for details see Tomassini et al., 2017). The gray-shaded area represents the standard error of the mean. The black horizontal bars indicate significant time points. Right, topography of the predictive value of theta phase for perception at −1.4 s and at -0.1 s. Significant channels are marked by bigger black circles.

Overall, the current evidence demonstrates that visual rhythms are not only phase-reset by external, attentional-capturing, cues but they can be locked to internally-generated motor events even of non-ocular nature, with functional consequences for perception. Yet, this putative visuo-motor oscillatory coupling exhibits complex temporal, spatial and spectral features.

Some variability has been reported in the exact modulation frequency across studies and participants. Research on attention mechanisms, has proposed that an 8-10 Hz visual sampling rhythm is divided (cycle-by-cycle) across space so that each location is sub-sampled at a rate which scales inversely with the total number of attended locations. Theta-range (4-5 Hz) rhythmicity in visual sampling is, in fact, primarily reported when two different locations\objects are simultaneously attended (Fiebelkorn et al., 2013, 2018; Helfrich et al., 2018; Jia et al., 2017; Landau et al., 2015; Landau and Fries, 2012; Re et al., 2019). Apparently, the movement-locked effects do not comply with this rule. Despite differences in visual task (detection\discrimination or segregation\integration), number of locations to be attended (one\two\multiple) and eccentricity of the stimuli (foveal\peripheral), saccade-locked (Benedetto and Morrone, 2017; Hogendoorn, 2016; Wutz et al., 2016) and hand-locked (Benedetto et al., 2016; Tomassini et al., 2017, 2015) rhythmicity has been generally observed in the delta (~2-4 Hz; with one exception, see Bellet et al., 2017) and theta (~4-6 Hz) range, respectively. Saccadic scan of the world is typically performed at a rate of about 2-3 saccades per second (Findlay and Gilchrist, 2008; Morrone and Burr, 2009; Rucci et al., 2018). One can argue that the perceptual modulations merely reflect the inherent sampling frequency imposed by the oculomotor system. In other words, perceptual periodicities might match the preferred frequency of the effectors involved in the sensorimotor behavior. Alternatively, as already mentioned, delta\theta-band rhythmicity may reflect a common attention-based clocking mechanism, which governs jointly both perceptual sensitivity and movement initiation (Fiebelkorn et al., 2019).

However, both these lines of reasoning do not fit equally well the case of hand movements which, in contrast to eye movements, do not show any clear temporal organization in natural behavior and do not (at least anatomically) mediate the actual sampling of visual information.

Many factors may indeed contribute to the frequency variability, including individual specificities (Benedetto et al., 2017, 2016; Fiebelkorn et al., 2013; Gulbinaite et al., 2017; Ho et al., 2017; Samaha and Postle, 2015; Tomassini et al., 2015) and task difficulty (Babu Henry Samuel et al., 2018; Chen et al., 2017). A fascinating field of future investigation will be understanding whether this diversity, both across tasks and subjects, effectively indexes functional differentiation. This will probably also help in gaining important insights into the functional relevance of this phenomenon and its possible context- and task-dependent modulation.

To clarify the functional role of this sensorimotor synchronization mechanism it is also important to consider whether it is domain-general. The existing literature addressing the rhythmic nature of perception has been traditionally focused on vision (see VanRullen, 2016). Nevertheless, a few studies have reported oscillatory modulations also in tactile (Ai and Ro, 2014; Baumgarten et al., 2015) and auditory (Hickok et al., 2015; Ho et al., 2017) perception, suggesting that rhythmicity may be a general (amodal) organizing principle. However, the strength of the oscillatory modulations varies from study to study, and it has been particularly challenging to demonstrate their presence for audition. Small changes in the experimental conditions (as the inclusion of acoustic noise or binaural presentation) may – in fact – mask the perceptual oscillation (VanRullen et al., 2014; Zoefel and Heil, 2013). Evidence of phase modulations are obtained also in cross-modal and multisensory studies, reinforcing the suggestion that neural oscillations may play a role in synchronizing signal processing between different sensory modalities (Lakatos et al., 2007; Mercier et al., 2015; Romei et al., 2012). So far, action-locked perceptual oscillations have only been reported for visual stimuli, although for movements executed by different effectors (eyes, hands). The effector-independence strongly points to a mechanism which transcends the anatomo-functional links between the sensory and motor systems involved. Nevertheless, it does not exclude that this phenomenon may be a peculiarity of vision. Indeed, the sensory modalities largely differ in their anatomo-functional interplay with the motor system. Because of the anatomical co-localization of sensors (retina, skin) and effectors (eyes, limbs), both vision and somatosensation own deep functional interconnections with the oculomotor and skeletomotor system, respectively. Differently, audition does not share the relevant sensory organ with any effector and for this reason it is rather independent from overt ‘sensory-gathering’ motor routines. Yet, despite audition being less obviously coupled with the motor system than vision and somatosensation, many pieces of evidence have uncovered a substantial motor contribution to the neural processing of auditory (e.g. Morillon and Baillet, 2017) and, in particular, speech (e.g. (D’Ausilio et al., 2009; Park et al., 2015) information.

Extending the investigation of the present phenomenon to other, non-visual, domains could thus prove a valuable tool to identify the anatomical and/or functional architectures that possibly constrain its implementation, and eventually clarify the specific computational/functional needs it might fulfill.

In the following sections we will discuss different hypotheses on how this sensory-motor oscillatory coupling might be achieved, with primary reference to the visual modality, and what functions it might subserve.

## Action-perception coupling: possible mechanisms and functional role

The new evidence gathered in humans has revealed some key features of the movement-locked neuronal and corresponding visual rhythmicity which prompt to partly revise the potential functional role of these modulations (Melloni et al., 2009; Schroeder et al., 2010). First, this phenomenon is not exclusive of the oculomotor system, but it also involves the hand effector which is anatomically and functionally decoupled from the visual receptor. This means that the oscillatory coupling is established independently of any intrinsic link between the motor and the sensory system. Secondly, it is observed for arbitrary sensory-motor contingencies, i.e., concurrently performed, but functionally unrelated, visual and motor tasks. Third, it is not a transient phenomenon, but an anticipatory, long-term modulation which precedes movement onset by ~1 s. This finding excludes that the final motor output (muscle contraction or reafference from body motion) may be itself the true synchronizing event and instead points to a hidden endogenous source. Finally, it occurs in the absence of any overt rhythmicity, either in motor behavior or in sensory stimuli. Hand movements (e.g. reaching, grasping, object manipulation), differently from other ‘sensory-gathering’ motor behaviors (e.g. visual exploration, locomotion, whisking, sniffing, licking), do not even manifest rhythmic patterns in natural scenarios.

Altogether, this suggests that the functional significance of this mechanism may go far beyond the idea that motor signals merely ‘support’ the sensory function by promoting timely suppression and enhancement of sensory excitability to enable perceptual stability (Melloni et al., 2009).

A first step towards understanding the genesis and, possibly, the functional role of this phenomenon requires answering the following questions: when exactly during the cascade of neural events leading up to action execution is this visuo-motor synchronization achieved? And what mechanism is responsible for this synchronization?

The studies already described have started to address these questions by delineating the spatiotemporal and spectral features of the visuo-motor oscillatory coupling, but they did not reveal the directionality of this coupling: is it the motor activity that drives the rhythmic visual modulation at the time of action planning\performance or, conversely, is it an intrinsic visual rhythm that yokes motor activity, cyclically dictating the probability of spontaneous movement initiation? Alternatively, are both motor and visual processes regulated by a shared rhythmic source?

Evidence suggests that motor functions, like sensory ones, are governed by underlying rhythmic processes indexing fluctuating states of neuronal excitability. Voluntary movements tend to be timed according to preferential phases of the ongoing oscillations (Bates, 1951). Behavioral studies have reported non-uniform, periodic, distributions of movement onset times (Dehaene, 1993; Latour, 1967; Treisman et al., 1992; White and Harter, 1969) and rhythmic fluctuations of reaction times following sensory cues (Huang et al., 2015; Song et al., 2014). This evidence is corroborated by neurophysiological findings showing systematic associations between the phase (and amplitude) of neuronal oscillations within the theta\alpha range and response speed (Bollimunta et al., 2008; Drewes and VanRullen, 2011; Hamm et al., 2010; Kienitz et al., 2018; Kirschfeld, 2008; Linkenkaer-Hansen et al., 2004).

However, given that the movements are externally-triggered, it is difficult to disentangle whether the rhythmical modulation in reaction times originates from oscillations in the sensory system (i.e., at the input stage) or in the motor system (i.e., at the output stage).

By probing directly corticospinal excitability, Transcranial Magnetic Stimulation (TMS) studies provide more compelling evidence that neuronal oscillations actually entail cyclic modulations of the motor system excitability. Indeed, motor evoked potentials (MEPs) are modulated not only by the amplitude (İşcan et al., 2018; Keil et al., 2014; Mäki and Ilmoniemi, 2010; Schulz et al., 2014) but also by the pre-TMS phase of ongoing oscillations at both peripheral (i.e., muscle activity; Keil et al., 2014, van Elswijk et al., 2010) and cortical level (Berger et al., 2014; Keil et al., 2014; Khademi et al., 2018). The use of neuromodulation techniques, such as transcranial Alternating Current Stimulation (tACS), in combination with TMS, have further shown that entrained, in addition to ongoing, beta-band oscillations affect MEPs size in a phase-dependent manner (Guerra et al., 2016; Nakazono et al., 2016; Raco et al., 2016; Schilberg et al., 2018).

Interestingly, the ongoing activity within the motor system, even at its most peripheral level (i.e., the muscles), shows early modulations by sensory stimulation. Visual stimuli, for example, elicit time-locked recruitment of neck and upper-limb muscles at very short latencies (< 100 ms; Corneil et al., 2004; Gu et al., 2016; Pruszynski et al., 2010) and reset the phase of low-frequency muscle oscillations (Wood et al., 2015). Multiphasic event-related responses to salient auditory and somatosensory stimuli can be detected in the motor output (i.e., in the force produced by isometric contraction) and these responses are coupled in time and amplitude to corresponding EEG evoked-potentials to the same stimuli (Novembre et al., 2018). Notably, the stimulus-locked responses observed in the force are neither startle-like, nor reflexive, suggesting a flexible, context-dependent, sensorimotor 'resonance' mechanism (Novembre et al., 2018).

Sensory stimuli not only affect peripheral motor activity but also modulate phase dynamics in an extended sensorimotor cortical network (Besle et al., 2011; Bressler et al., 1993; Hirvonen et al., 2018; Lobier et al., 2018; Mercier et al., 2015). Interestingly, multimodal stimuli promote stronger local as well as inter-regional low-frequency (delta\theta) phase synchronization between sensory and motor areas compared to unimodal stimuli (Mercier et al., 2015), and the strength of the sensorimotor coupling positively scales with response speed (Hirvonen et al., 2018; Mercier et al., 2015). A recent study on monkeys further shows that the oscillatory synchronization between motor and somatosensory areas is subject to learning-dependent plasticity (Arce-McShane et al., 2016), reinforcing the idea that phase alignment may be a general strategy to establish effective neuronal information transfer (Engel et al., 2001; Fries, 2015; Palva and Palva, 2018; Womelsdorf and Fries, 2006).

Another set of evidence showing perception-to-action oscillatory modulations stems from motor priming paradigms. Visual stimuli can automatically activate specific motor plans; this immediate motor facilitation of the primed action is, however, shortly replaced in time by its inhibition (Eimer and Schlaghecken, 2003; Sumner and Brandwood, 2008), with reaction times for two competing actions fluctuating with anti-phasic theta-band periodicity for almost 1 s (Huang et al., 2015).

Whereas all these pieces of evidence suggest that sensory stimuli, and in particular visual stimuli, can trigger changes in motor-related oscillatory activity and sensorimotor phase synchronization (and corresponding motor performance), a recent study shows that the reverse is also true. Tomassini and D'Ausilio (2018) characterized the spectrotemporal dynamics of visual perception ensuing externally-controlled activation of the somatomotor hand system which allowed bypassing of the endogenous component involved in action programming and execution (Tomassini and D'Ausilio, 2018). To this aim they exploited the peripheral stimulation of the median nerve: in fact, despite not targeting specifically and uniquely the motor cortex, this stimulation activates with nearly the same latency both the somatosensory and motor subdivisions of the hand which are known to constitute a single functional unit in the control of movement (e.g. Lemon, 2008). They observed strong and long-lasting (1 s) alpha oscillations in visual perception following the median nerve stimulation. Phase-locking of visual rhythms is thus not conditional on the formulation of an intention to move or of a motor plan but may also ensue from the passive recruitment of the somatomotor system.

We have seen multifaceted findings showing that the sensory and motor systems exert reciprocal influences through modulation of the ongoing brain dynamics.

The evidence available so far is not conclusive as regards the origin of the visuomotor synchronization and its underlying brain circuitry. However, a few clues suggest that motor-related activity might play a key role. Notably, visuomotor synchronization (as indexed by movement-locked rhythmicity in perception) seems to be automatically established whether movement is freely-initiated (Bellet et al., 2017; Benedetto and Morrone, 2017; Tomassini et al., 2015), internally-timed (Tomassini et al., 2017) or externally-triggered (Hogendoorn, 2016; Wutz et al., 2016), i.e., in conditions demanding very different mechanisms for the control of movement onset. Any phasic modulation of spontaneous movement initiation due to ongoing fluctuations in motor excitability should be independent of the task-specific constraints placed on movement timing. However, in the study by Tomassini et al., (2017), it is shown that the visuomotor oscillatory coupling evolves with a different temporal dynamic when participants are asked to perform the movement at two different time intervals (1.5 and 2.3 s) after cue presentation. This difference (which is not a trivial consequence of cue presentation) strongly suggests that theta oscillatory dynamics may be itself a constituent part of movement preparation, at least of the neuronal process that is specifically involved in the active (task-related) control of movement timing. The rhythmic coupling between the visual and motor system is thus not invariant to the current motor state, suggesting that it may structure dynamically the functional interplay between the two systems, enabling the timely incorporation of sensory information within the ongoing motor plan.

## Multiple clocks, one time?

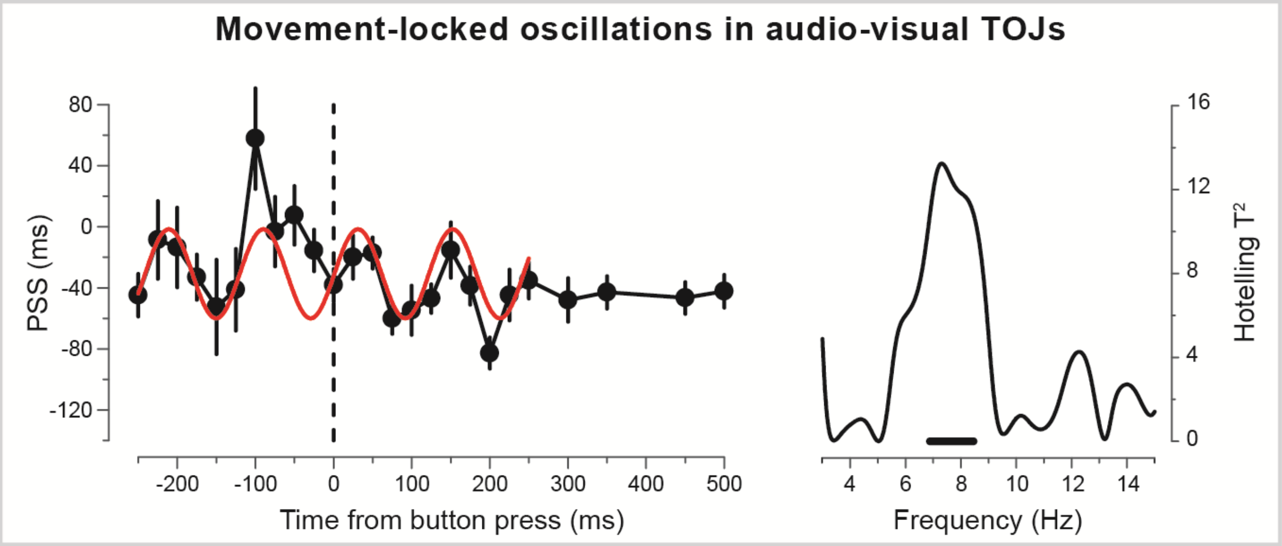
Natural behavior commonly relies on multimodal sensorimotor loops, whereby the sensory stream of information continuously updates the current motor programming, and the motor system, in turn, generates predictions about the upcoming sensory data. Multimodal signals, however, travel at different speeds along the sensory pathways. Alongside, the perceived timing of sensory events varies across modalities and features of the sensory stimulation (Burr et al., 2011; Harrington et al., 2011; Johnston et al., 2006; Kanai et al., 2006; Tomassini et al., 2011). How does the brain deal with temporally-inconsistent signals and achieve an efficient sensorimotor control?

Besides affecting sensitivity, it is known that brain oscillatory activity is strictly related to the temporal features of the stimuli (Baumgarten et al., 2015; Cecere et al., 2015; Kononowicz and van Rijn, 2015; Kösem et al., 2014; Milton and Pleydell-Pearce, 2016; Parker et al., 2014; Samaha and Postle, 2015; Wiener et al., 2018). For instance, recent evidence points to a direct mapping between neuronal oscillations and temporal windows of integration\segregation (Ronconi et al., 2017; Ronconi and Melcher, 2017). Interestingly, the probability of either integrating or segregating two stimuli alternates as a function of the phase of neuronal rhythms (Ronconi et al., 2017), and these rhythms are aligned to saccadic fixation onset (Wutz et al., 2016). This latter evidence suggests that movement-related modulations of oscillatory activity may also have an impact on the temporal processing of the stimuli.

Multiple lines of evidence strongly suggest that the motor system is critically involved in timing-keeping functions (e.g. Merchant and Yarrow, 2016), as attested by its consistent recruitment in both implicit and explicit temporal tasks (Merchant et al., 2013; Wiener et al., 2010). It has been shown that motor areas effectively tune the ongoing activity of sensory areas to incoming rhythmical inputs, yielding perceptual improvements (Morillon and Baillet, 2017). The motor system can thus convey temporal predictions to the sensory system through rhythmic top-down modulation (Arnal and Giraud, 2012; Morillon et al., 2015; Schubotz, 2007). Movement also has a powerful influence on perceived time. Visual timing, for example, is compressed and\or dilated around the execution of both eye (Binda et al., 2009; Morrone et al., 2005) and hand movements (Haggard et al., 2002; Hagura et al., 2012; Park et al., 2003; Tomassini et al., 2018; Tomassini and Morrone, 2016). This movement-related temporal modulation has been observed also for other sensory domains, such as for tactile stimuli, suggesting that it is a general phenomenon (Tomassini et al., 2014, 2012; Yarrow and Rothwell, 2003).

One recent study by Benedetto et al. (2018) further shows that audio-visual temporal order judgments (TOJs) undergo rhythmic fluctuations (at around 7-8 Hz) time-locked to a button press action (figure 4). The modulation does not affect temporal sensitivity (precision of the judgements) but the temporal bias, i.e., whether the visual stimulus is perceived ahead or behind of the auditory stimulus (in line with the neuronal phase effects on audio-visual perceived simultaneity reported by Ikumi et al., 2018; and Kösem et al., 2014). This suggests that processing resources and\or speed may rhythmically alternate between the visual and the auditory modality and this alternation may be temporally synchronized to the ongoing motor processing. The motor system seems to be able to orchestrate the processing of multiple signals, that are relayed at different speeds along the central nervous system, by exerting endogenous control over the brain oscillatory dynamics.

The existence of a mechanism that keeps perception and action finely synchronized is suggested by a recent study by Tomassini et al., (2018).  The authors assessed interval estimation for a brief visual stimulus (150 ms) that was shown (at random times) while participants were performing rhythmic finger tapping (at 1 Hz). Perceived visual time undergoes distortions which are locked to the motor acts; time is compressed close to the onset of finger taps and expanded in-between successive taps. Remarkably, the temporal dynamic of these perceptual distortions scales linearly with the timing of the motor tapping, so that maximal time expansion is always experienced at the center of the inter-tap interval, independently of the natural (trial-by-trial) variability in the tapping rate (see figure 4). Perceptual time is thus anchored to the internally-dictated rhythm of motor production. These results indicate that even if the sensory and motor clocks might be distinct, their functioning is nevertheless strictly coupled.



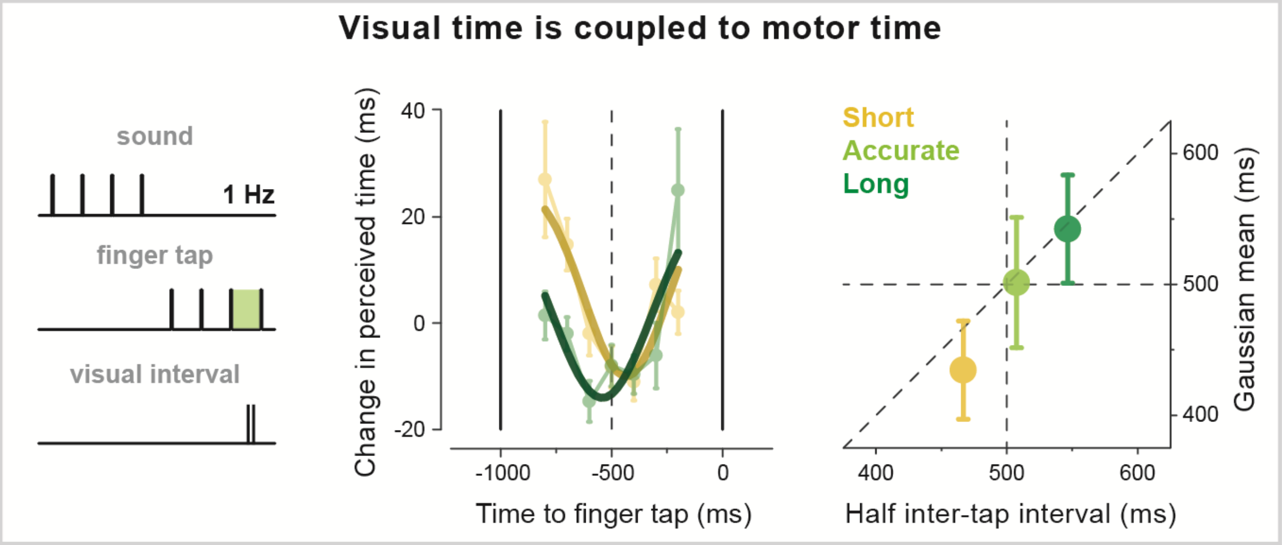


Figure 4. Box on top: left, time course of the Point of Subjective Simultaneity (PSS± 1 SEM) for audio-visual stimuli, expressed as a function of movement onset (from Benedetto et al., 2018). The red line shows the best sinusoidal fit (frequency =8.2 Hz). Right, spectral components in the time course of PSS that show phase-consistency across subjects (see Benedetto et al., 2018 for methods details). The horizontal thick line indicates the significant frequencies ($p < 0.05$). Box on bottom: left, schematic of the experimental procedure from Tomassini et al., 2018. Four auditory tones were played at 1 Hz. Participants were asked to continue the

sequence of tones by pressing a button four times with their right index finger at the same rate as the sound presentation. At random times between the 3rd and the 4th button press (marked in green), two visual flashes (5 ms each) were presented separated by a variable temporal interval (probe). Participants reported whether the probe interval was shorter or longer compared with the standard interval (150 ms, presented at the beginning of each block; not shown). Center, time courses in perceived duration aligned to the 4th tap and best-fitting Gaussian functions for trials in which participants tapped at a faster rate, yielding short inter-tap intervals (yellow) and at a slower rate, yielding long inter-tap intervals (dark green). Right, the mean of the best-fitting Gaussian function (indexing the latency of maximal perceived time expansion) is plotted against half of the inter-tap interval for short (yellow), accurate (light green), and long (dark green) trials. The diagonal indicates that maximal perceived time expansion occurs halfway between the two consecutive finger taps.

The movement-locked rhythmicity in perception may thus be the by-product of an oscillation-based mechanism whereby the dynamics of sensory processes can be plastically scaled to be synchronized with the ongoing motor processes, effectively closing-up the sensorimotor loop.

**Conclusions**

Growing evidence shows that brain oscillatory dynamics is anticipatorily phase-locked to movement onset (Popovych et al., 2016; Staudigl et al., 2017; Tomassini et al., 2017) and that this very same activity affects perceptual (Tomassini et al., 2017) as well as memory (Staudigl et al., 2017) performance, i.e., it *is* behaviorally relevant. Strikingly, similar movement-locked rhythmicity in behavioral performance is reported irrespective of the effector, movement type and task demand; for example, with saccades (Benedetto and

Morrone, 2017; Hogendoorn, 2016; Wutz et al., 2016) and micro-saccades (Bellet et al., 2017), reaching movements (Tomassini et al., 2015), isometric contraction (Tomassini et al., 2017), button press (Benedetto et al., 2016; Zhang et al., 2019) as well as with freely-initiated (Bellet et al., 2017; Benedetto and Morrone, 2017; Tomassini et al., 2015), internally-timed (Tomassini et al., 2017), externally-triggered movements (Hogendoorn, 2016; Wutz et al., 2016) and also exogenous activation of the somatomotor hand system (Tomassini and D'Ausilio, 2018).

These findings outline a new and promising view on the intimate interconnection between sensory and motor functions and its possible neurophysiological substrate.

The evidence available so far is restricted to low-level, near-threshold, sensory tasks (e.g. visual contrast detection) and arbitrary sensory-motor contingencies (concurrently performed, but functionally de-coupled, sensory and motor tasks). Although this points to an automatic and domain-general mode of operation of sensorimotor systems which may sub-serve core functions, its general relevance and functional significance are still not clear. Indeed, if oscillatory mechanisms do shape the sensorimotor information flow, their functional impact should be amplified for more complex behaviors that truly depend on fast and accurate information exchange between the sensory and motor system for their successful accomplishment.

The study of the role of oscillatory mechanisms in action-perception coupling is at its beginning and understanding the degree of (domain-) specificity, plasticity and context-dependency of these mechanisms are only some of the many aspects which call for further investigation.

The existing evidence certainly reveals that perception and action are inherently coupled even when their coordination is not directly enforced by the task at hand. Their study cannot thus prescind from a unified perspective whereby perception is conceived as a *sensorimotor* phenomenon for which attempting to identify univocally the origin either within the motor or the sensory system is most probably an intrinsically ill-posed problem.

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