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Author

De Kock, Rose

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Timing in Motion: The Impact of Motor Manipulations on Time Perception

By

ROSE DE KOCK
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DAVIS

Approved:

Wilsaan Mychal Joiner, Chair

Julie Schweitzer

J. Faye Dixon

Joy Geng

Timothy Hanks

Committee in Charge

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Abstract

Interval timing, a subcategory of time perception, is central to healthy cognitive functioning in everyday life. Findings have emerged highlighting a critical role of the motor system in supporting timing functions. Evidence for its importance stems from both neural and behavioral data; timing tasks are shown to activate motor brain regions such as the supplementary motor area, even when the tasks do not require overt motor responses. On the other hand, behavioral studies have shown that incorporating movement into timing tasks leads to changes in timing precision and accuracy, depending on the manipulation. Here, we examined the role of movement in time perception across three studies. Our first study was driven by prior findings that movements covering longer distances are perceived as lasting longer than movements covering shorter distances. We tested whether restricting arm movement via an external manipulation (i.e., a viscous movement environment) would lead to the same effect. As viscosity increased, perceived time was shortened, supporting our hypothesis. This study also highlighted that movement parameters do not need to be self-modulated to induce movement-related distortions. Our second study was motivated by a gap in knowledge surrounding movement-timing relationships: while existing studies had demonstrated that adding movement to timing tasks exerted changes to performance, the process by which participants judged the duration of their own movements was unknown. We compared accuracy and precision performance between three interval timing conditions: auditory, movement, and combined. The novel findings from this study were that movement intervals were underestimated compared to auditory intervals, and importantly, that timing accuracy was highest when these two signals were combined. Finally, we investigated the role of movement in timing for adults with ADHD. Studies of timing in this population are relatively uncommon and yield heterogeneous results, yet it is a topic of interest due to consistent patient reports of experiencing difficulty with time management. Our research previously found a beneficial effect of movement on timing precision in a sample of healthy adults, and here, we tested whether this would be the case for

participants with ADHD. Surprisingly, a movement-related improvement in timing was not found for either the ADHD or control group. We suggest this may be due to the within-subjects manipulation and block design of the study, where participants experienced interleaved blocks of movement and non-movement trials. This contrasts with our prior study in which participants were assigned to a movement or non-movement group, and the observed benefit may have been dependent on the continuous exposure to the movement condition. Additionally, our sample size was relatively small, and potential differences may require more data to uncover. However, a notable finding was that participants with ADHD significantly underestimated time intervals compared to controls, which had not been previously established in the duration range that we tested. In summary, our studies addressed novel research questions about the qualities of movement that affect timing, how movements are timed in isolation and combined with concurrent sensory signals, and how movements interact with timing in adult ADHD. These advancements pave the way for further research on the nuances of movement-timing relationships, and how they influence human cognition on a broader scale.

*Dedicated with love,
to Edwin and Ria De Kock, in memoriam.*

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Chapter 1: How movements shape the perception of time

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Abstract

In order to keep up with a changing environment, mobile organisms must be capable of deciding both where and when to move. This precision necessitates a strong sense of time, as otherwise we would fail in many of our movement goals. Yet, despite this intrinsic link, only recently have researchers begun to understand how these two features interact. Primarily, two effects have been observed: movements can bias time estimates, but they can also make them more precise. Here we review this literature and propose that both effects can be explained by a Bayesian cue combination framework, in which movement itself affords the most precise representation of time, which can influence perception in either feedforward or active sensing modes.

Time and movement are intertwined

Continuous interaction with a dynamic world requires organisms to make precise temporal measurements of sensory input and directed motor output. As such, sensorimotor coupling is vital in multiple levels of organization in the nervous system, from spinal reflexes to complex motor sequences [1]. These intertwined sensorimotor processes have potential implications in the study of time perception [2]; however, the link between action and time perception has, until recently [3], been relatively unexplored. Current studies demonstrate that action exerts a

wide range of effects on subjective time by biasing (i.e., affecting accuracy; see Glossary) or improving sensitivity (i.e., precision) of estimates and that these effects are not restricted to concurrent movement, but can exhibit robust effects before and after movement. Notably, a unifying account does not yet exist for these effects - a challenge for current models of timing (Box 1). Here, we propose a basic framework to base future studies upon; specifically, we suggest that movement provides a new channel of temporal information that is (i) evaluated by its reliability and (ii) integrated into temporal estimates optimally, in line with Bayesian cue combination (Box 2). This is a prominent idea in multisensory research that has been demonstrated previously in time perception across distinct sensory modalities [4].

Motor systems are invoked during time perception

Given the necessity of time and movement in everyday interactions, it is not surprising that the brain areas involved in these processes greatly overlap (Figure 1A). Timing relies on several brain systems traditionally thought to be dedicated to motor control [5,6], and that are activated during timing tasks where no overtly timed motor response is required (Figure 1A). The main cortical area implicated in temporal processing is the supplementary motor area (SMA). The SMA is often split into two main components by the anterior commissure: SMA-proper, bordering the primary motor cortex, and pre-SMA, located more anteriorly [7] and has been shown to be chronotopically organized in a rostrocaudal gradient, in that rostral clusters of neurons encode shorter durations and caudal clusters encode longer durations ([8]; see Figure 1B). More specifically, the SMA-proper is implicated in motor timing tasks, timing of single events [9], timing of shorter durations, stimulus-driven movements, and motor preparation [7], whereas the preSMA is implicated in perceptual timing tasks [10,11], sequence processing [12], self-initiated movements, response inhibition, timing of longer durations, and task switching. The SMA also appears to have a gradient for time and space, with SMA-proper neurons encoding longer duration actions in navigating the environment [13]. Further, recordings in the SMA of non-human primates demonstrate duration tuning of individual neurons [14], as well as neurons

that encode the categorical boundary between duration ranges that are predictive of temporal categorization [15].

Box 1. Models of time perception Numerous models have been developed over the past 50 years to describe and explain timing behavior. Of these, the most influential has been Scalar Expectancy Theory (SET), which proposes that timing results from a tripartite process in which an internal clock emits and accumulates pacemaker pulses, proceeding at a particular rate and variability, then compares the accumulated amount to a remembered criterion before making a ratio-based decision [131]. An alternative to this is the Behavioral and Learning Theory of Timing (BeT & LeT), which instead suggest that temporal accumulation emerges as a successive chaining of distinct behavioral 'states' with variable intervals between them [132,133]. More recent work conceives timing as a time-adaptive opponent drift-diffusion model (TopDDM) process, in which opponent populations of neurons generate a rate-adaptable process that elapses with the perceived interval [134]. Alternatively, recurrent neural network (RNN) models suggest that activity develops across stereotyped state-space trajectories, allowing for the measurement of distinct time intervals [108,109,135]. Across all of these models, bias and variability can be seen as arising from shifts in pacemaker rate or neural firing trajectories, as well as the variance/shape of those trajectories. For example, SET would posit a change in pacemaker rate/variance, whereas BeT/LeT might suggest changes in the number of states, or the variance of inter-state intervals. Similarly, TopDDM might suggest a shift in drift rate or its variance while timing, whereas RNN models would suggest changes in the speed or variance of the trajectory. Thus, a critical question for models of timing that posit a sensorimotor component, is if they can recapitulate movement-related changes in timing, both in conditions where movement is critical for the timed response (motor timing) or not critical (perceptual timing).

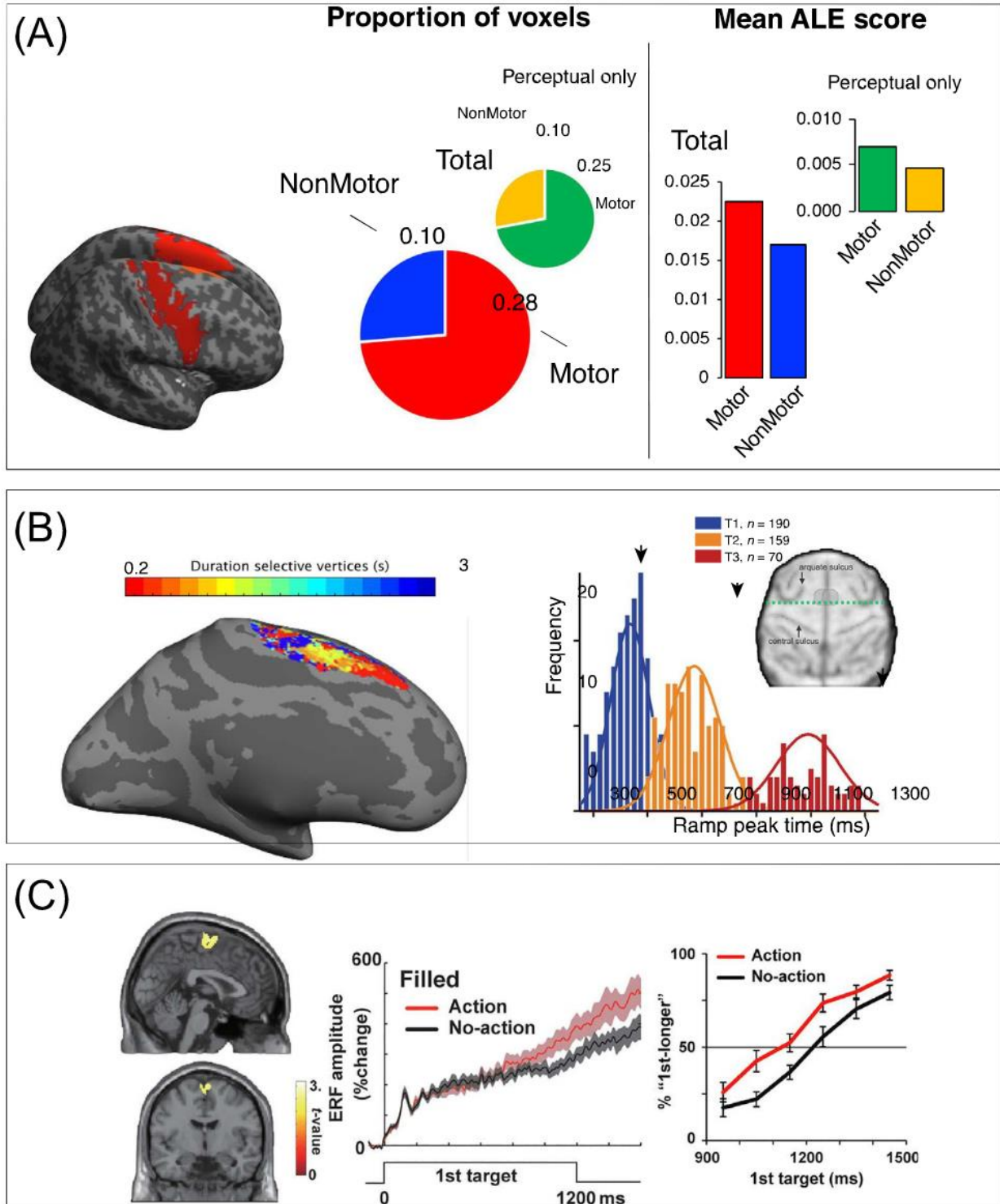


Figure 1. The motor system is involved in time perception. (A) Results from a recent meta-analysis of neuroimaging time perception studies (results adapted, with permission, from [5]) exhibiting greater activation likelihood in motor cortical regions (red highlights, from AAL atlas for SMA and precentral gyri) over nonmotor ones. Specifically, motor regions exhibit a higher

mean proportion of significant voxels than non-motor regions, even when motor timing tasks are excluded (inset); additionally, mean activation likelihood estimation (ALE) values within motor regions are typically higher than those in nonmotor regions (right side), again when excluding motor timing studies (inset). (B) The SMA exhibits tuning for duration and categorization. Left, high-resolution 7T fMRI 'chronotopy' of SMA in a time discrimination task reveal rostrocaudal gradients of activation. Adapted, with permission, from [8]; right, single-unit recordings of SMA neurons in primates performing a time bisection task reveal tuning preferences for the bisection point of three different interval ranges. Adapted, with permission, from [15]. (C) Movement-induced changes in time perception, while a subject engages in an action, are linked to increases in SMA activity. Adapted, with permission, from [29].

Subcortical motor systems, such as the basal ganglia (BG) and cerebellum also play a prominent role in timing. Innervation of the BG by dopamine neurons has demonstrated a close link with timing functions [16,17]. In animals, dopamine availability is strongly linked to the direction of temporal distortions; artificially increasing or decreasing striatal dopamine leads to overestimation and underestimation of time intervals, respectively [18]. Recent work has demonstrated a dissociation between these sub-cortical structures (BG and cerebellum) for timing in rhythmic and single-interval contexts [19]; further, both structures have been found to impact activity putatively within the SMA [20,21]. These findings suggest that time perception is instantiated in motor circuits between the SMA and subcortical regions, via cortical-striato-thalamic connections.

Given the strong overlap between motor and timing regions in the brain, it should be expected that disorders of movement also exhibit timing impairments [21,22]. Importantly, these impairments persist in perceptual timing tasks when movement is irrelevant or unnecessary [23]. For example, Parkinson's Disease is associated with timing that is both less precise and less accurate, although deficits are heterogenous [24]. Huntington's Disease patients display similar timing deficits, including greater response variability in interval (i.e., absolute) and beat-

based (i.e., relative) timing [23]. Additional timing deficits have been observed in patients with Tourette's Syndrome [25], Essential Tremor [26], Cerebellar Degeneration [20], Dystonia [27], and those with lesion damage affecting motor regions [28].

Concurrent movements bias time perception

Despite the involvement of motor regions in time perception, until recently movements were not specifically studied in the context of timing. Models of time perception typically set movements to represent the end-point of a timed process, with motor variance existing as a nuisance to be partialled out (Box 1). Yet, early evidence of this relationship came in the form of the chronostasis phenomenon, wherein saccading to a target induced a stereotyped expansion of visual time [30]. Post-action temporal expansion was also found for tactile feedback after manual movement to a target [31], auditory stimuli following a saccade [32], and spontaneous blinking [33]. A separate finding, intentional binding, describes a process by which an action and its sensory consequence are 'pulled' towards each other in time [34,35]. More recent work suggests that both phenomena may reflect distinct aspects of the same underlying process [36]; that is, the combination of disparate sensory and motor representations [37]. These representations may be combined in a manner that is also optimal with respect to Bayesian computations [38]. Yet, we note that both are examples in which timing is causally tied to the sensory consequences of actions, which we suggest are distinct from studies of explicit timing [39].

Within the realm of explicit timing, initial evidence that actions could lead to shifts in perceived time came from work demonstrating that, when asked to perform a time reproduction task, the length of that interval is longer when its initiation is triggered by a subject's action [40]. Yet, while this established a link between motor timing and movements, a connection with perceptual timing would not come until a later study [41] in which the duration of tactile vibrations applied to the finger while performing a large single-movement lift were dilated compared to being at rest.

Several follow-up experiments replicated this effect, demonstrating that the duration of an avatar hand performing a finger movement that was congruent with the movement was similarly dilated. This latter finding was similar to another motor timing study in which subjects reproduced auditory durations encoded while watching videos of broad hand gestures; longer-distance hand movements were associated with longer reproduced intervals [42].

An additional number of studies have also found that concurrent movements during time perception can compress or dilate time estimates (Figure 2) depending on various factors; the most significant contributor seems to be the influence of magnitude. It is implicitly understood that short, fast, or near movements take less time, and long, slow, or far movements take more time. This implicit knowledge may be at least partially instantiated in motor circuitry [43] and is necessary to evaluate one's movements in the environment [44]. Therefore, studies that use actions that imply a particular movement magnitude could bias the perception of other magnitudes. For example, sensory events that appear in reachable space are perceived as having a shorter duration than those in unreachable spaces [45].

Further, when subjects performed either short and long, or slow and fast finger hyperextensions, as well as near and far hand reaching movements while judging the duration of auditory stimuli, perceived time was dilated when longer, slower, or farther movements were performed ([46]; Figure 2E). By contrast, another study found when subjects performed either slow, medium, or fast hand circles while judging the duration of visual stimuli, faster hand movements were associated with a compression of perceived time [47]. However, in this case, subjects were restricted to making movements within a constrained area. As such, faster hand movements may have led to compression due to a reduced sampling of the environment; indeed, slow, deliberate movements have been shown to provide more information than faster ones [48,49], within a certain limit [50]. Other studies have also shown that, within the same area of space, slower movements lead to time dilation effects [42,46]. More recently, we performed a series of experiments in which subjects were required to move a robotic handle to

explore a flat workspace while performing either a temporal bisection task or time reproduction task with auditory intervals [51]. Crucially, increasing resistance (i.e., viscosity) of the robotic handle resulted in shorter movement paths and subsequently shorter perceived durations. Computational modeling further suggested that the time compression effects occurred at the level of perception, rather than decision or production levels.

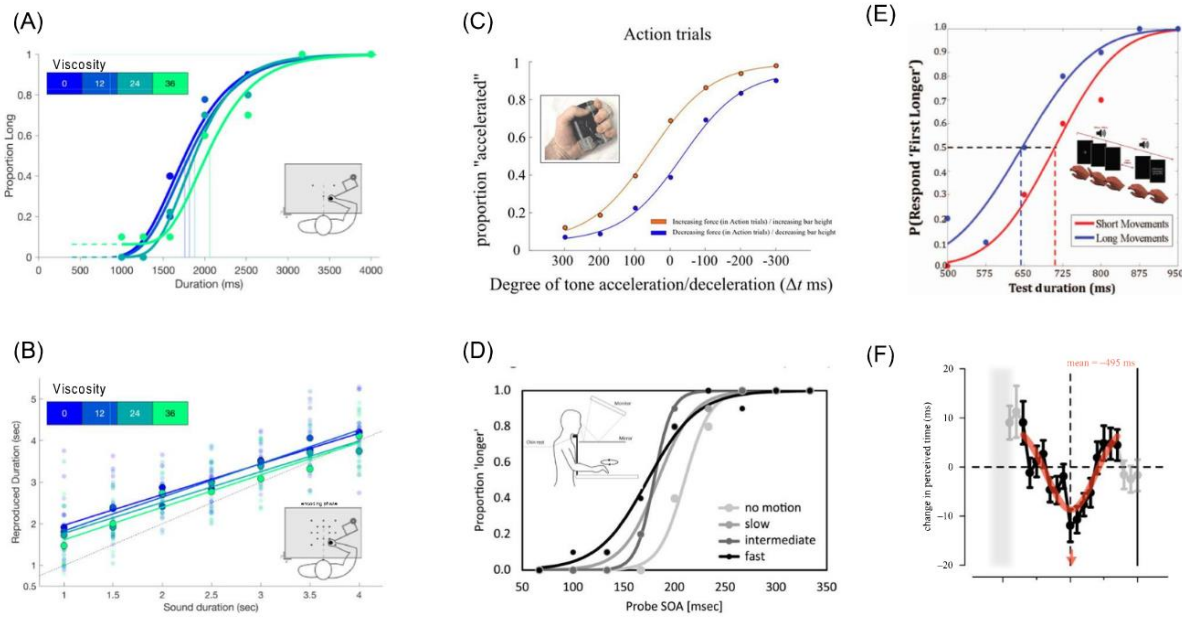


Figure 2. Concurrent movements bias time perception. (A) While categorizing auditory tone lengths, increasing the viscosity of a concurrently moved robotic arm leads to shorter perceived durations. (B) Similarly, reproduced time intervals experienced with greater viscosity are also shortened. (C) Holding a force gripper with increasing/decreasing force while judging tone sequences as accelerating/decelerating enhances the separation between perceptual judgments. (D) When judging time intervals while performing circular movements behind an occluder at different speeds, faster speeds lead to shortened perceived time intervals. (E) When performing a finger hyperextension at different speeds, longer movement lengths lead to longer perceived intervals. (F) Similarly, when tapping with the index finger, concurrently presented time intervals are lengthened at the halfway point between finger taps, but shortened at times

closest to the preceding or upcoming finger tap. Data from (A,B): [51]; (C): [55]; (D): [47]; (E) [46]; and (F) [52], with permission.

Other possible explanations for movement-related temporal biases include at what point during the movement the interval occurred [52], the type of stimuli [53], and the sense of agency of the movement [54]. For example, when subjects performed a synchronization-continuation task using finger taps- during which a separate visual temporal interval to be judged occurred randomly during the continuation sequence- the direction and strength of the bias depended on the point during the finger tap the interval occurred ([52]; Figure 2F).

Concurrent movements improve time perception

In addition to the work cited above showing the biasing effects of movement, there is also evidence that concurrent movements can enhance timing (Figure 3). This secondary finding is an essential component of Bayesian cue combination, in which greater precision leads to greater bias. In one study [56], subjects were more precise timing auditory intervals when the stimulus onset was determined by the subject (Figure 3B). Further studies [57] found that subjects were more precise timing auditory tones when they freely moved compared to remaining stationary. In both bisection and reproduction experiments, precision improved without affecting accuracy (Figure 3A), independent of movement strategies or proximity to choice targets. Further, time estimates could be decoded from the movements, suggesting that movements were actively engaged in the timing process, rather than reflecting its output. A similar finding was recently observed for facial muscles recorded during a visual temporal bisection task [58]. Similarly, in a recent experiment, rats learned to approach a goal location after a fixed interval (7 seconds in most experiments) to obtain a reward. They were positioned on a small treadmill that began moving backward during the interval period. Over many trials, rats learned to keep time by employing a stereotyped 'wait-and-run' strategy - they started at the front of the treadmill, allowed it to take them backwards, and ran to the goal location. Rats using

this strategy displayed higher accuracy and precision than rats not using the strategy (Figure 3E). Additionally, accuracy and precision were lower when treadmill movement was omitted; however, trials with more movement were more accurate, demonstrating that movement improved timing overall, but performance was highest when temporal regularities in the external environment could be used in tandem with movement [59]. In another rodent experiment, rats performing a temporal bisection task adopted stereotyped head movements as measured by motion tracking, with virtually no between-subject similarities. Importantly, movement patterns, even early in the trial or prior to stimulus onset, were predictive of the eventual choice [60]. A similar finding in humans is that when tracking a moving target with the hand, the perceived duration is also more precise [61], particularly when the target moves in a compatible way with human movement [62].

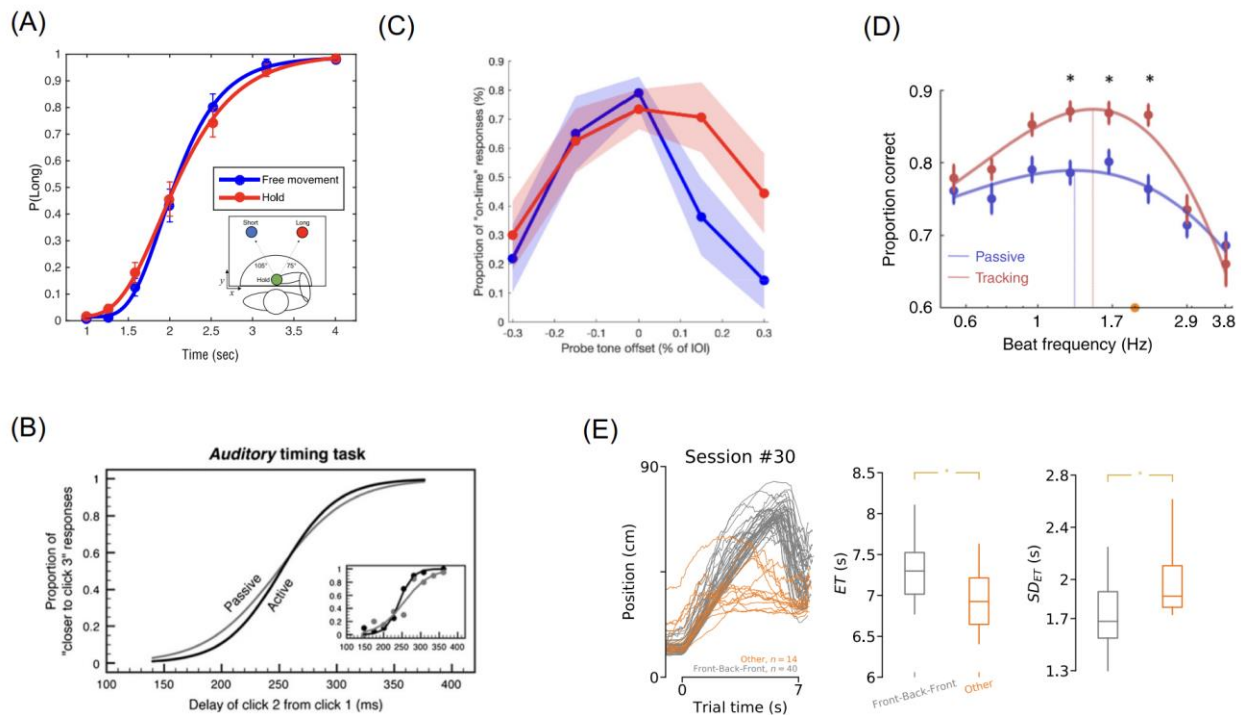


Figure 3. Concurrent movements enhance timing. (A) When freely allowed to move a robotic arm while categorizing auditory time intervals, the perception of those intervals is more precise (lower coefficient of variation) than when the arm is held in place during listening. (B) When

discriminating auditory intervals, perception is more precise when interval onset is initiated by the subject than when it is presented at a fixed onset. (C) When tapping along with an auditory beat (blue trace), subjects are more precise at detecting deviant tone intervals of different durations. (D) Action improvements in beat perception additionally show greater accuracy and reduced variability at a preferred tempo of 1.5Hz. (E) In rats, when trained to walk along a moving treadmill to a target at fixed time (7s), rats that develop a stereotyped movement pattern (gray traces) exhibit improved accuracy and greater precision of the entry time (ET). Asterisks refer to significant effects at $P < 0.05$, from the original sources. Data from (A): [57]; (B) [56] (C) [64]; (D) [67]; and (E) [59], with permission.

In addition to enhancing precision for interval timing, research on beat-based timing demonstrates several advantages of sensorimotor synchronization in timing rhythmic stimuli [63]. More specifically, actively tapping along with a rhythm leads to greater accuracy [64–66] and precision [67] at detecting rhythmic deviants.

These considerations are additionally interesting between movements that have explicit temporal properties versus emergent temporal properties, whereby rhythmic properties in the former require 'event timing' -explicit temporal representations of each cycle (e.g., tapping) -and in the latter, temporal properties emerge as a byproduct of other motor goals (e.g., maintaining constant velocity during circle drawing; [68]). Further, emergent timing (in a rhythmic context) is thought to evolve from an initial explicit representation (e.g., during the first cycle of circle-drawing) that is thereafter replaced by emergent timing [69]. So far, we have highlighted instances of emergent motor 'strategies' that aided in concurrent interval timing, and although these timing distinctions have not been investigated in the majority of studies, they are an interesting future research direction.

Of note, improved timing abilities during action have additionally been observed in individuals with highly trained motor skills, such as elite athletes [70], expert drummers [71], and professional dancers [72]. This highlights the plasticity of time-keeping that evolves with motor experience; indeed, research in children also suggests that temporal concepts are built upon an understanding of actions and their consequences [73]. Further, movement training also enhances other perceptual discrimination abilities [74,75]. Conversely, subjects trained to discriminate a time interval become better at reproducing it with a motor action [76].

Pre-action and post-action effects on timing

In addition to the effects of concurrent action, there are also distinct effects on perceived duration during pre-action and post-action periods, yet with notable inconsistencies. For pre-action periods, in some cases durations are compressed [77–79] and in others dilated [29,80,81]. Various factors lead to these differential effects, including whether the temporal stimulus is a filled interval or an empty interval [29,81] as well as the intended direction of a planned movement [79].

It has been suggested that pre-action visual processing is accelerated to maximize opportunities for stopping or changing a planned action, thus leading to longer perceived intervals. This idea was originally supported when subjects perceived filled visual intervals as longer during preparation of ballistic reaching movements during a temporal discrimination task [80]. Additionally, when viewing flickering visual stimuli during the same period, flicker frequencies were perceived as slower, and subjects displayed increased detection rates for flickering letter displays compared to when passively viewing the stimuli. Notably, this effect appears to only extend to filled intervals, whereas empty intervals are not affected [81]. In addition, magnetoencephalography (MEG) activity revealed ramping activity in the SMA during filled intervals only (Figure 1C) as well as asymmetric suppression of visual 10Hz alpha rhythms. This interaction between motor and visual factors reveals a selective role of alpha rhythm for neural communications across visual, motor, and time-processing regions [29].

In contrast to these pre-action effects, temporal shifts are also observed after actions are initiated [30,32,82]. Often, motor plans are executed with a goal and predicted sensory consequences. As such, these consequences are initially processed separately from externally-generated sensory signals in the brain [83]. Additionally, sensory feedback is used to evaluate the accuracy of goal-directed movements and calibrate internal models to perform future movements more effectively [84–87]. These specialized evaluation mechanisms accompanied by selective suppression or amplification of sensory signals may have implications in time perception. Taken together, the discussed temporal shifts induced during pre- and post-action periods are indicative of dynamic neural encoding of time with respect to action onset. This is compatible with general principles of motor control, such as anticipatory and predictive pre-action signals, and evaluative and corrective post-action signals [86] - measures that have rarely been examined in the context of explicit timing. Given the nuances of action-locked temporal distortions, dynamical system analysis techniques may elucidate trial-by-trial contributions of evolving movement states to perceived time. These have been used in motor control to understand the evolution of motor 'states', both behaviorally [88] and neurally [89]. Dynamical systems models have also been used to understand interval timing [90] and beat-based timing [91], but only recently to study the interactions of movement and time perception [3,92]. This would be a productive area for future research, and highlights the necessity of collaborative efforts with complementary motor control and timing expertise.

A framework for movement and time

As described above, movement effects on explicit time estimates, both perceived and produced, can lead to both biases and enhancements under particular conditions. Additionally, these effects are predicted using a Bayesian cue combination framework (Box 2). Yet, cue combination has traditionally been formulated as one in which disparate channels of sensory information are combined to a unified percept. In our framework, movement itself serves as an

additional channel for duration information. Accordingly, the brain integrates the statistics of body movements, which are affected by the speed, length, direction, and area covered. As such, the sampling of positional information in space provides a vector [93] 'readout' of elapsed time across a neuronal population. Further, given the high temporal fidelity and precision of motor movements, with some estimates below 10ms [94,95], the variance of movement time estimates is also predicted to be very low. Indeed, motor neurons have demonstrated tuning properties related to both upcoming and preceding movement in time at different lags relative to the present moment [96]. Further, SMA firing rates themselves exhibit multidimensional trajectories that provide tracking and scaling of movements [97], suggesting this region is continuously evaluating the temporal statistics of the environment. This final point is critical; previous studies have demonstrated a 'modality-appropriateness' effect in time perception, such that, when measuring a time interval presented with multiple sensory modalities, time estimates gravitate towards the modality with the lower variance [98]. Across sensory modalities, auditory time estimates have been shown as more precise than visual time estimates [99], with tactile estimates in between [100]. Yet, movements have been found to affect visual, tactile, and auditory estimates, suggesting that movements afford a precision that is better or at least as precise as any other sensory domain.

We suggest that a Bayesian cue combination process can explain disparate findings across the literature. In some ways, these effects appear to be universal to time estimates; movement-related effects have been found to influence sensory time estimates across sensory domains, task designs, and also at both sub- and supra-second intervals. The latter effect is particularly relevant, given that sub-second interval timing has been shown to rely more on subcortical structures traditionally associated with movement [5]. By contrast, many common movements span the multi-second domain, and so movement-related effects on longer intervals may not be surprising. Nevertheless, the above literature highlights the fact that not all movements are equal with respect to influencing time. Indeed, we suggest time can be affected

differently across movement direction, rhythmicity, effector, and vigor. These differences may arise from the natural variance of particular movements [101], which may relate to how commonly they are employed [102]. Notably, these differential effects of movement parameters may arise as a result of magnitude-based priors leading to a bias in time estimates in certain directions (e.g., shorter movements take less time than longer movements; [103]).

As stated above and in Box 2, Bayesian cue combination can provide a method by which noisy sensory estimates are combined optimally. In this case, movements shift timing by pulling estimates towards their (more precise) duration. No studies that we are aware of have investigated how well humans can time the duration of their own movements, however, according to MLE predictions, movement timing should have a precision that is equal to or better than auditory timing precision. A further prediction is that, when the more precise modality becomes less reliable, its weighting in the combined estimate will decrease. Thus, if movements are made less reliable or uncertain, they should have less of an influence on time estimates from other modalities. Similarly, the cue combination framework for multisensory timing holds most strongly when the sensory modalities demarcating time intervals are filled rather than 'empty' [104]. This distinction may explain why movement effects are inconsistent or absent when the interval being timed is also empty [81]. By contrast, during an empty interval, the motor system is likely still active, and so one may predict that empty intervals should instead lead to stronger movement-related effects. The finding that this prediction does not hold has implications for the neural instantiation of cue combination effects for movement and time.

Box 2. Bayesian cue combination Bayesian Cue combination is a proposed mechanism by which the brain can combine noisy sensory estimates from different modalities. It serves as an extension of Bayesian Decision Theory, in which noisy sensory estimates are perceived as draws from a likelihood function with a certain mean (μ) and variance (σ^2) that are then combined with a prior distribution of previous estimates to form a posterior estimate of the stimulus. In the case where two sensory modalities are presented, the sensory estimates are combined optimally using Maximum Likelihood Estimation (MLE), in which the variance of the multisensory estimate distribution is the product of the unisensory variances divided by their sum (see Figure 4B in main text). Further, the mean of the multisensory estimate is

determined by a weighted sum of the unisensory means, where the weights are crucially, and inversely, related to the unisensory variances. In this way, the multisensory estimate mean is always 1) closer to the unisensory estimate of whichever modality is more precise, and 2) itself more precise than either of the unisensory estimates alone. Applications of Bayesian Cue Combination have been used to explain how the brain combines estimates of visual and haptic stimuli [136], and auditory and visual stimuli [137]. For time perception, Bayesian Cue Combination has also, to varying degrees of success, described and predicted behavior in the timing of auditory and visual stimuli [104], and visual and tactile stimuli [138] in humans. Applications of Bayesian Cue Combination have also been used to explain temporal averaging in rats [139]. For movement-related effects, this framework can explain both precision and biasing effects (see Figure 4C in main text).

Neural implementation

If Bayesian cue combination can explain movement-related effects on time, then how are these effects implemented in the brain? We outline two possibilities (Figure 4D, Key figure). First, as described above, motor structures predominate neural timing systems, and so one possibility is that movements lead to changes within these motor circuits themselves, most notably the SMA, possibly by sharpening duration or category-tuned neurons, which are driven by sensory and motor responses, or by altering the speed and variance of state-space trajectories. This possibility, which we term Feedforward Enhancement, suggests that motor effects on time occur within motor regions themselves in an adjunctive manner [29]. Indeed, given that the motor system is active during timing, regardless of whether subjects are moving or not [11,105], timing computations may be intrinsically driven and shaped by motor activity. Previous work demonstrating timing responses in motor and premotor cortices has also suggested that the motor system may develop internal models of predictable events in time [106], for use in guiding future movements with increased temporal precision [87]. Additional evidence for Feedforward Enhancement comes from neural recordings in non-human primates, demonstrating motor system trajectories of neural firing rates that are used to encode the duration of intervals [90,107]. These trajectories may be employed across a variety of timing tasks and domains [108,109]. Yet, given this involvement, why would concurrent movements

enhance timed responses, rather than hinder them [110]? One possibility is that, when remaining immobile, subjects are faced with a variety of possible, competing movement trajectories, whereas during movement the brain can exploit corollary feedback from movements to dynamically update neural trajectories [111]. Movement preparation offers a similar reason for enhancement, as the specific movement to be made is being prepared over alternatives, which shifts motor cortex activity into a more active state [112]; recent work further suggests movement preparation shifts spontaneous M1 activity into an optimal subspace for engaging in the intended movement [111]. Further, recent modeling work using feedforward neural networks has demonstrated that reinforcement learning agents can learn to time intervals by self-generating idiosyncratic movement patterns that can be exploited as a temporal measurement [113].

Altogether, Feedforward Enhancement would predict that movement-related timing effects depend on motor cortex activity and, crucially, on corollary feedback from movements. One prediction from this hypothesis is that altering proprioceptive information about a subjects movements should alter or eliminate movement-related timing effects. For example, if a subject were moved automatically without any volition, then no movement-related effects should exist. Similarly, if a subject lost all access to feedback regarding movements, then movement-related effects should similarly be reduced. Previous work with deafferented patients has shown a disruption in motor timing abilities which is stabilized in presence of visual feedback [114,115]. Further, movement-related effects on time persist even when limb position is occluded [51,57].

However, while the presence of motor activity during non-motor timing is evident, this does not necessarily mean that motor-related effects on timing are occurring there. Indeed, work with recurrent neural networks demonstrates that timed responses can be 'learned' by any neural region [116,117]. As such, motor activity during perceptual timing may be a byproduct of the way in which time intervals are learned [73], owing to the development of the motor system in primates as a critical node for acquiring cognitive skills [118]. Therefore, a second possibility

is that motor activity provides recurrent influence back on the sensory regions themselves, thus leading to more precise, yet biased neural firing in sensory cortices. This possibility, termed Active Sensing [119], has more empirical support from other domains, where motor movements have been found to alter and enhance [120,121] responses in sensory regions (Figure 4D).

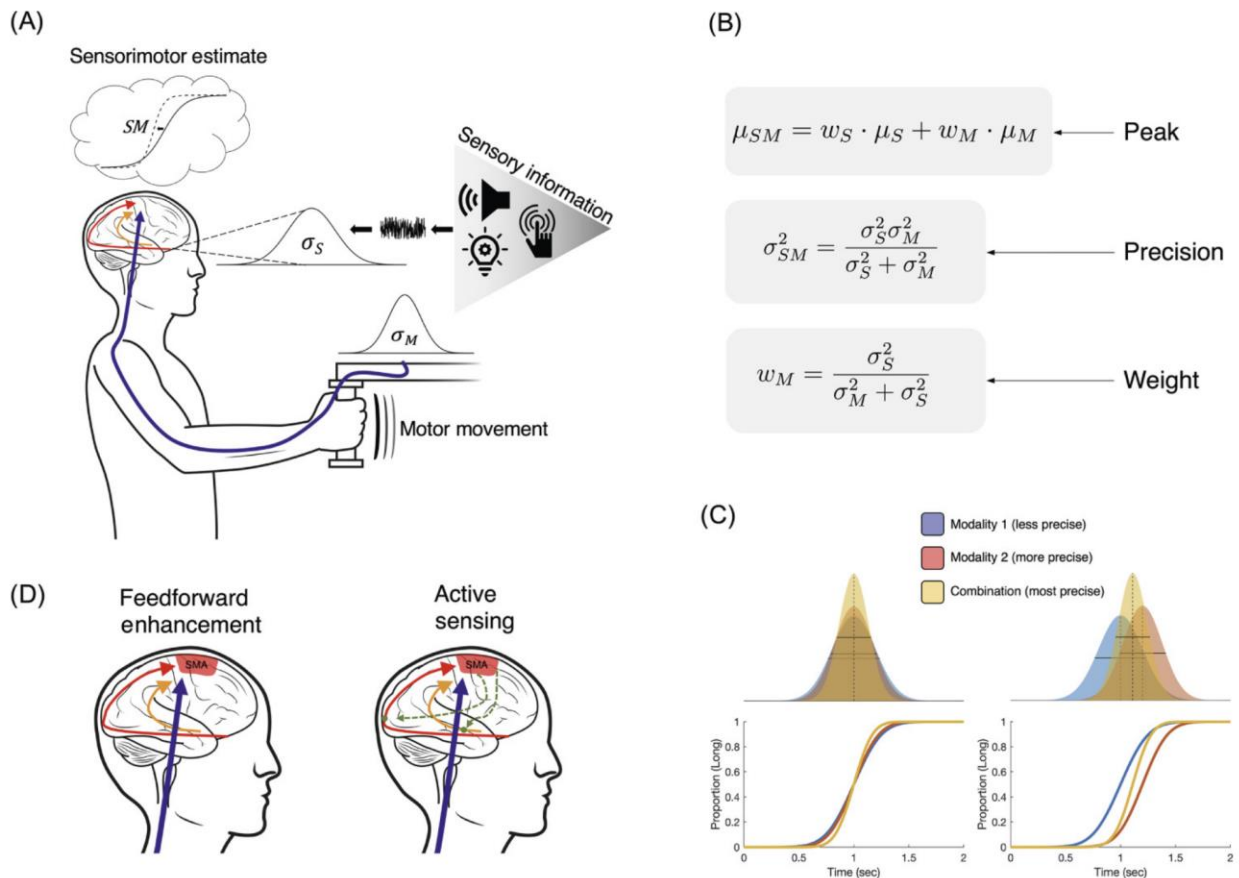


Figure 4. (A) Enhancement and bias effects in time perception can be explained by a cue combination framework (Box 1), in which movement provides the greatest temporal fidelity. When subjects measure sensory time intervals (S), presented in different modalities (auditory, visual, or somatosensory), this information is transformed into a noisy estimate with variance σ_S that is transferred along sensory pathways to the SMA and accompanying motor circuitry. Concurrent movements, here of a robotic arm, confer a second duration estimate (M) that is perceived with greater reliability and lower variance σ_M . (B) Both estimates are combined via cue combination equations to form a sensorimotor estimate of duration (SM) that is both more

precise, yet biased towards the movement duration estimate. (C) Cue combination framework for combining two signals from different modalities with different levels of precision (top: likelihood distributions for each modality and combination; bottom: psychometric curves for a standard time bisection task). Left panels display the case when both modalities have the same mean; right panels display the case with different means. (D) In a Feedforward Enhancement mode, movement directly influences time estimates occurring within the SMA and associated motor regions; Conversely, in an Active Sensing mode, sensory responses are influenced via feedback from movement-related regions (green broken traces).

Under an Active Sensing framework, sensory responses will be altered by motor activity evoked by concurrent movements while estimating time, which will in turn further influence motor-related timing activity. This hypothesis more closely matches experimental data from other domains, in which movements lead to substantial changes in sensory activity [122] that can further enhance neural responses to sensory stimuli [123]. Further work in humans has demonstrated tight linkage between sensory detection and motor activity [124]. For example, walking in an open environment can enhance peripheral visual contrast sensitivity [125], and recent work has demonstrated that movement plans can be decoded from sensory regions associated with the consequence of those movements [126].

For movement-related effects on explicit timing, the Active Sensing hypothesis matches some experimental findings. For example, the Active Sensing hypothesis predicts that movement-related effects critically depend on activity within sensory cortices. This prediction explains why movement-related effects appear to be strongest for time intervals that are 'filled' rather than 'empty' [29]. Further, recent evidence demonstrating that motor regions rhythmically enhance sensory responses to perceived rhythms according to preferred frequency bands, additionally supports the Active Sensing hypothesis [67]. Yet, movement-related effects have

also been observed for empty intervals, although less consistently across different modalities [56]. Additionally, interesting work has shown that the sensory consequences of planned movements elicit less sensory-evoked activity [127], which should therefore lead to shorter perceived durations [128], whereas the opposite is actually observed. These inconsistencies suggest that both Feedforward Enhancement and Active Sensing hypotheses need to be further examined to determine which can best instantiate cue combination and movement-related effects.

Concluding remarks

In this review we have introduced a basic framework of how movement information can bias timing while improving its precision, from the overlap of neural systems to behavioral correlates. We note that this area of study is in its early stages: most movement-timing studies have examined effects of brief [53], discrete [30], or ballistic movements [80], and have tightly controlled motor variables of interest in laboratory settings. Naturally, these come with some limitations. The multi-effector and multisensory qualities of our everyday experiences call for more ecologically valid experimental paradigms. For example, future studies could focus on time perception outcomes for longer-scale continuous movements, movements with varying velocity profiles (e.g., biological vs. non-biological motion), and movements with uncertainty or competition between possible action plans [129]. Additionally, it would be worthwhile to study how timing relates to whole-body movement parameters (e.g., locomotion/gait, rotation, and head movement) and multi-effector motor sequences. High-level movement characteristics like these have not yet been investigated in detail for timing, and with the emergence of sophisticated motion tracking and virtual reality environments, the feasibility of studies with greater ecological validity is increasing [130].

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Chapter 2: Slowing the body slows down time perception

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Abstract

Interval timing is a fundamental component of action and is susceptible to motor-related temporal distortions. Previous studies have shown that concurrent movement biases temporal estimates, but have primarily considered self-modulated movement only. However, realworld encounters often include situations in which movement is restricted or perturbed by environmental factors. In the following experiments, we introduced viscous movement environments to externally modulate movement and investigated the resulting effects on temporal perception. In two separate tasks, participants timed auditory intervals while moving a robotic arm that randomly applied four levels of viscosity. Results demonstrated that higher viscosity led to shorter perceived durations. Using a drift-diffusion model and a Bayesian observer model, we confirmed these biasing effects arose from perceptual mechanisms, instead of biases in decision making. These findings suggest that environmental perturbations are an important factor in movement-related temporal distortions, and enhance the current understanding of the interactions of motor activity and cognitive processes.

Introduction

Interval timing is an essential part of survival for organisms living in an environment with rich temporal dynamics. Biologically relevant behaviors often require precise calibration and execution of timed output on multiple levels of organization in the nervous system (Cisek and Kalaska, 2010). For example, central pattern generators produce basic locomotion in many organisms and yield balanced, rhythmic motor output via the oscillatory properties of inhibitory

interneurons (Guertin, 2009). At greater levels of complexity, many behaviors rely on the explicit awareness of time (Buhusi and Meck, 2005). Subjective time is not always veridical, however; in fact, across many organisms, it is subject to distortion (Malapani and Fairhurst, 2002). As described by Matthews and Meck, 2016, temporal distortions can arise from changes in perception, attention, and memory processes, and are proposed to be directly related to the vividness and ease of representation of a timed event. Interestingly, action properties can also influence perceived time. For example, it has been shown that subjective time on the scale of milliseconds to seconds is influenced by movement duration (Yon et al., 2017), speed (Yokosaka et al., 2015), and direction (Tomassini and Morrone, 2016). More specifically, timed events accompanied by arm movements that are short (Yon et al., 2017), rapid (Yokosaka et al., 2015), or directed toward the body (Tomassini and Morrone, 2016) undergo compression.

These studies grant insight into the importance of action in the context of timing, but they are limited by focusing solely on volitional modulation of movement parameters. Often, organisms encounter changes in the environment that dramatically affect the way motor plans are executed. When these perturbations are encountered, organisms use feedback information to update current and future movement plans (Shadmehr et al., 2010). In the following experiments, we sought to modulate the parameters of movement distance and speed by introducing changes in the movement environment itself rather than through instruction or task demands. Participants were required to time auditory tone intervals while moving a robotic arm manipulandum through environments with varying degrees of viscosity. This was tested first in a temporal categorization task, then in a temporal reproduction task with a new group of participants. If it is the case that time perception is biased by movement distance then limiting movement by applying viscosity should lead to underestimation of intervals. In our previous work (Wiener et al., 2019), we utilized a very similar free-movement categorization paradigm to study the effect of movement on time perception. Unlike the current study, this paradigm had no viscosity factor, but rather tested whether participants that were allowed to move during timed

intervals differed in performance from participants that were not allowed to move. Allowance of movement enhanced temporal perception by reducing variability (i.e. lower coefficient of variation). However, results observed in this study were mechanistically ambiguous. That is, we observed that temporal judgments were more precise with movement, but it was unclear whether this effect was driven by perceptual changes or modulation of decision properties (Figure 1a). Thus, in the current study, we sought to provide a more mechanistic explanation of our observed results by disentangling perceptual effects and ensuing downstream processes (choice selection in the categorization experiment, and measurement and estimation in the reproduction experiment). In the categorization experiment, we demonstrate that viscosity successfully decreased movement distance, and that this decrease was associated with underestimation of time intervals. We verified that this modulation was a result of interval timing and not a decision-related bias by applying a recently developed drift-diffusion model of timing (Balci and Simen, 2014). In the reproduction experiment, all participants tended to overestimate durations, but viscosity was related to decreased overestimation and greater central tendency. We utilized a Bayesian Observer Model (Jazayeri and Shadlen, 2010; Remington et al., 2018) to verify that this effect was a result of perceptual bias rather than increased noise in the measurement and production processes. Overall, these results suggest that movement distance has a direct influence on perceived interval length, regardless of whether this parameter is modulated by volitional or environmental factors.

Results

Experiment 1 - temporal categorization

In our first experiment, 28 human subjects engaged in an auditory temporal categorization task using supra-second intervals between 1 and 4s. Subjects were required to classify each interval as 'long' or 'short', compared to the running average of all previously experienced intervals. To classify each interval, subjects were required to move the arm of a robotic manipulandum to one of two response locations, counterbalanced between subjects.

Prior to tone onset, subjects were allowed a 2s 'warm-up' period, in which they were free to move the cursor around and explore the environment. During this period, the resistive force (f) against the manipulandum was gradually increased to reach a peak viscosity (v) of four possible levels (0, 12, 24, or 36 Ns/m² ; see Materials and methods); the viscosity remained at this level for the remainder of the trial (Figure 1b). Entry into the response location prior to the tone offset was penalized by restarting the trial, and so the optimal strategy was to move the cursor closer to the 'short' location, and then gradually move to the 'long' location as the tone elapses (Wiener et al., 2019). Consistent with this strategy, we found that the relative location of the hand at interval offset was closer to the short target for intervals at or under the middle of the stimulus set, but rapidly moved closer to the long target for longer intervals [$F(6,162) = 4.791$, $p < 0.001$, $\eta^2_p = 0.151$] (Figure 1—figure supplement 1A). However, no impact of viscosity was observed on relative hand position [$F(3,81) = 1.595$, $p = 0.197$], suggesting that movement had little impact on the ability of subjects to employ this strategy. One possible explanation for this lack of an effect is that the introduction of viscosity altered the optimal positional strategy across participants; indeed, external movement perturbation on choice reaching tasks similar to this one reveal that movement strategies change in response to additional effort (Burk et al., 2014). We further note that, in this task the position at offset did not guarantee that subjects would choose the closer response location. We further verified that our viscosity manipulation worked by observing a decrease in movement distances [$F(3,81) = 21.05$, $p < 0.001$, $\eta^2_p = 0.438$] and an increase in force applied to the arm with higher viscosities [$F(3,81) = 22.736$, $p < 0.001$, $\eta^2_p = 0.457$] (Figure 1—figure supplement 1A).

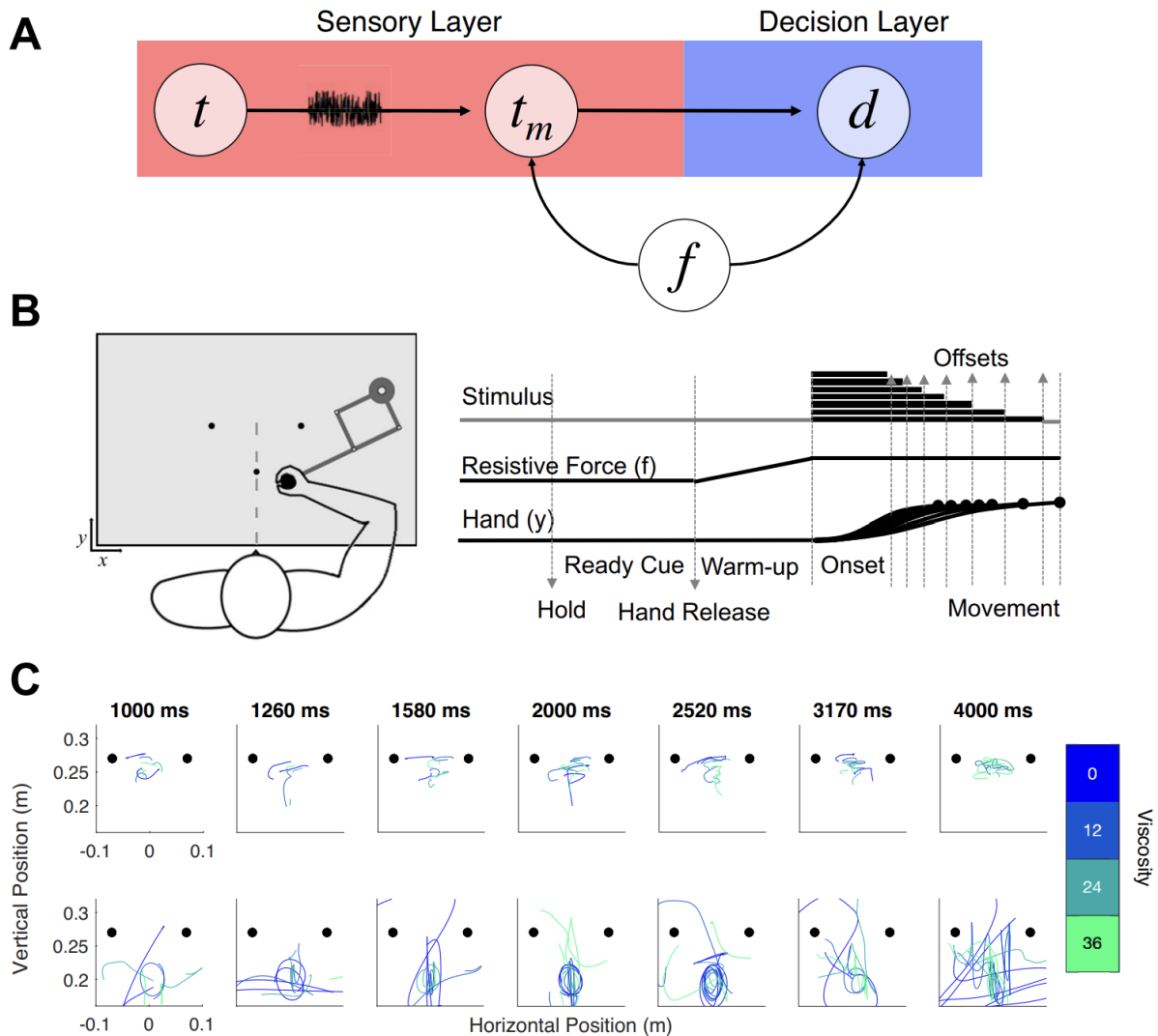


Figure 1. Hypothesis and design of Experiment 1. (A) Potential pathways in which movement (f) could influence timing. The first possibility is that f specifically alters the sensory layer, in which a stimulus presented for an amount of time (t) is perceived with noise as a temporal estimate (t_m); here, f could specifically alter the measurement process, either by shifting the way that estimate is perceived or by altering the level of noise. The second possibility is that f shifts the decision layer, such that decisions about time (d) are biased to one choice or another (e.g. more likely to choose ‘long’). (B) Task schematic of Experiment 1. Participants began each trial with the robotic handle locked in a centralized location. The trial was initiated by a warmup phase in which the hold was released and viscosity was applied in a ramping fashion until the target

viscosity was reached. Participants were allowed to move throughout the workspace during warm-up and tone presentation, and reach to one of two choice targets to indicate their response (Hand y data shows hypothetical paths to the chosen target). (C) Example trajectory data; each row displays sample trajectories from two subjects. The trajectories include movement during the tone for the seven possible tone durations for each of the four viscosities.

The online version of this article includes the following figure supplement(s) for figure 1:

Figure supplement 1. Additional effects for categorization and reproduction tasks.

Figure supplement 2. Individual differences in movement parameters for categorization and reproduction tasks.

Analysis of choice responses proceeded by constructing psychometric curves from the mean proportion of 'long' response choices for each interval/viscosity combination, and chronometric curves from the mean reaction time (RT) as well (Figure 2a and Figure 1—figure supplement 1). Psychometric curves were additionally fit with cumulative Gumbel distributions, from which the bisection point (BP) was determined as the 0.5 probability of classifying an interval as long. Analysis of the BP values across all four viscosities with a repeated-measures ANOVA revealed a significant effect of viscosity [$F(3,81)=3.774$, $p=0.014$, $\eta^2_p = 0.123$]. A further examination revealed this to be a linear effect, with BP values generally increasing with viscosity, indicating a greater tendency to classify intervals as 'short' [$F(1,27)=5.439$, $p = 0.027$, $\eta^2_p = 0.168$]; we further note that examination of a quadratic contrast did not reveal a significant effect [$F(1,27)=1.209$, $p=0.281$]. To further confirm this effect, we calculated slope values of a simple linear regression of the BP against viscosity across subjects; a non-parametric bootstrap (10,000 samples) of 95% confidence intervals demonstrated that slope values did not overlap with zero [0.3183 - 2.8563], indicating robustness of the effect. Analysis of RT values demonstrated faster RTs with longer perceived duration [$F(6,162)=38.302$, $p < 0.001$, $\eta^2_p = 0.587$], consistent with previous reports (Balci and Simen, 2014; Wiener and Thompson, 2015;

Wiener et al., 2019). This pattern is thought to reflect increased decision certainty associated with longer intervals; once an elapsed interval crosses the categorical boundary, subjects shift from preparing a 'short' choice to a 'long' choice, with increased preparation for longer durations. Additionally, a significant effect of viscosity was observed [$F(3,81)=14.684$, $p < 0.001$, $\eta^2_p = 0.352$]; however, the effect was variable across viscosities, with faster RTs for mid-range viscosities. No effect of viscosity was observed on the CV [$F(3,81)=0.377$, $p=0.77$; $BF_{10}=0.073$] (Figure 1—figure supplement 1).

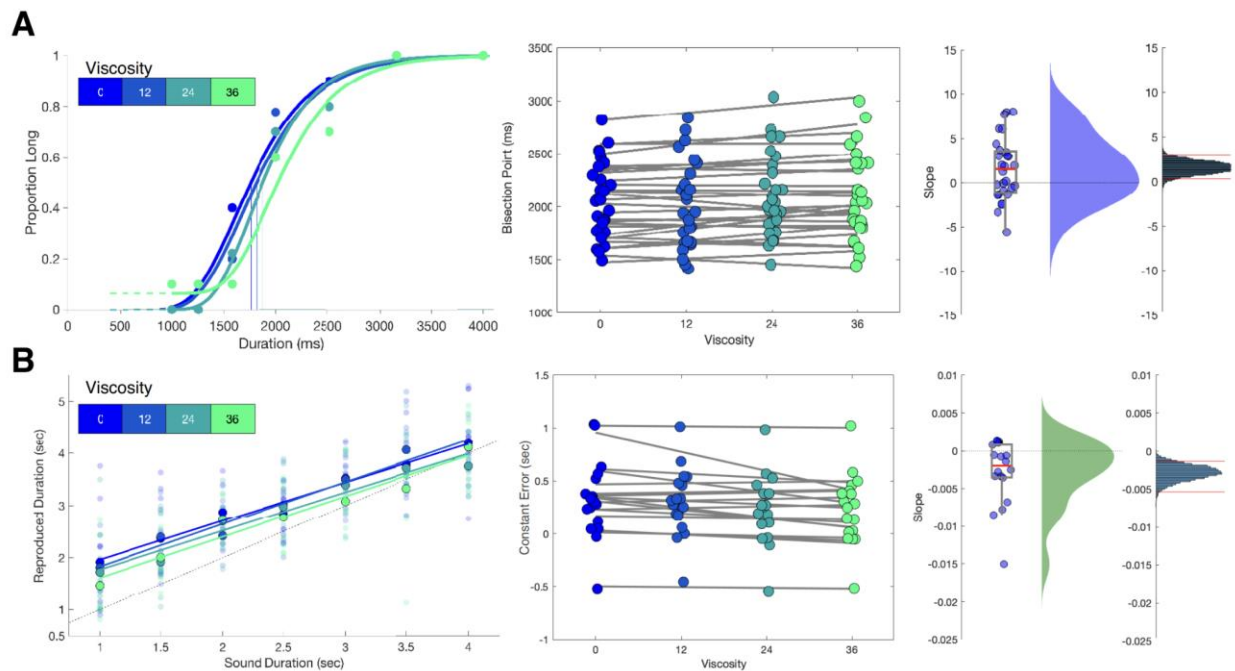


Figure 2. Viscosity shifts time responses. (A) Results from Experiment 1 (Temporal Categorization). Left panel: psychometric curves fit to response proportions for a representative subject exhibiting a rightward shift with increasing viscosity; vertical lines indicate the Bisection Point (0.5 probability of classifying 'long'). Middle panel: Bisection points for all subjects across viscosities; gray lines represent best fitting linear regressions. Right panels: boxplots and kernel densities of slope values for linear regressions, along with bootstrapped distributions of the mean slope (rightmost panel) with 95% confidence intervals. (B) Results from Experiment 2 (Temporal Reproduction). Left panel: Reproduction performance for a representative subject

exhibiting progressively shorter reproduced time estimates with higher viscosities; faded points represent single trials, solid points represent means, lines represent best fitting linear regressions. Middle panel: Mean Constant Error (difference between reproduced and presented interval) for all subjects across viscosities; gray lines represent best fitting linear regressions. Right panels: boxplots and kernel densities of slope values for linear regressions, along with bootstrapped distributions of the mean slope (rightmost panel) with 95% confidence intervals.

Influence of movement parameters

We further examined the impact of individual differences in movement parameters on the observed behavioral findings. As noted above, movement distance was successfully manipulated by imposing different environmental viscosities. However, we observed large inter-individual differences in the average distances moved by different subjects. That is, some subjects moved a lot, whereas some moved very little; notably, subjects were largely consistent in their movement distances across viscosity conditions (Figure 1—figure supplement 2A). Similarly, subjects who moved more also exerted more force in doing so; we further observed that the effect of viscosity on movement distance and force were correlated between subjects [Pearson $r = -0.73$, $p < 0.001$; Spearman $r = -0.88$, $p < 0.001$]. We further examined if the effect of viscosity on time perception was modified by individual differences in movement distance. Here, we found only a weak correlation between the effect of viscosity on movement distance and the bisection point [Pearson $r = -0.286$, $p = 0.1395$; Spearman $r = -0.35$, $p = 0.067$]. Similarly, the correlation between the effect of viscosity on force was also very weak [Pearson $r = 0.147$, $p = 0.45$; Spearman $r = 0.221$, $p = 0.25$], suggesting that the effect of viscosity did not covary with individual differences in movement distance or force.

While the above results suggested no between-subject difference in the magnitude of the effect, this does not preclude a within-subject influence. In our previous report (Wiener et al., 2019), we observed that subjects performing this task exhibited a more precise perception of time (lower CV) compared to subjects who performed a different version where the robotic arm

was fixed at the starting point for the duration of the interval. Although the present study allowed all subjects to move freely during the interval, we hypothesized that movement during the interval would interact with precision within-subject. To test this possibility, we performed a within-subject median split of the movement distance for each interval/viscosity combination and re-analyzed the psychometric curves for each viscosity condition. For the BP, we again observed an increase with viscosity [$F(1,27) = 5.936$, $p = 0.022$, $\eta^2_p = 0.18$], regardless of how much subjects moved [$F(1,27) = 1.397$, $p = 0.247$] (Figure 3a). For the CV, a significant interaction between viscosity and movement distance was observed [$F(1,27) = 7.694$, $p = 0.01$, $\eta^2_p = 0.222$], in which the CV was significantly lower when subjects moved more, but only when the viscosity was zero [$t(27) = -2.237$, $p = 0.034$, $D = 1.2$] (Figure 3b), and not for any other viscosity (all $p > 0.05$). This indicates that precision again improved with greater movement, but only when no impediments from a viscous movement environment existed.

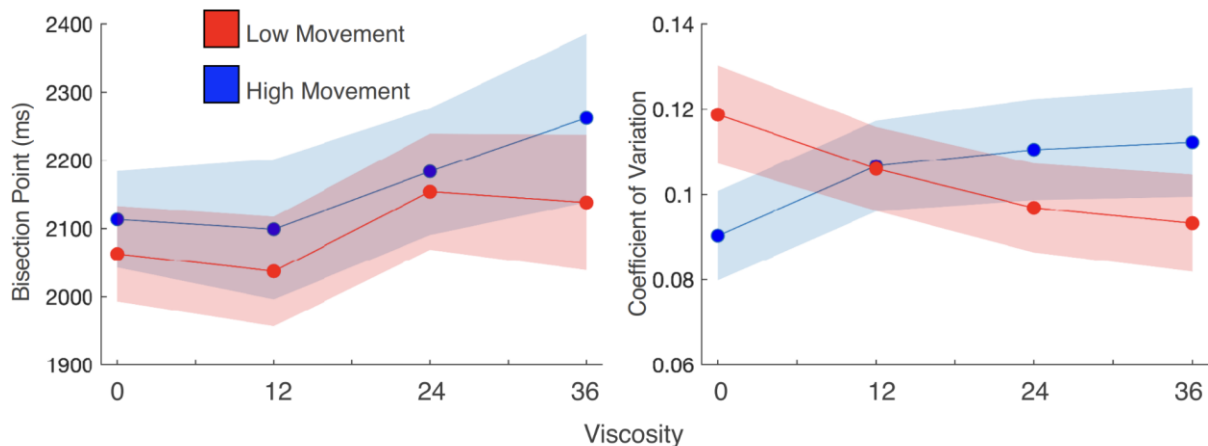


Figure 3. Movement speed does not change viscosity effects, but does influence precision. (a) Mean bisection points and (b) coefficients of variation for participant trials divided into high and low movement via a median split. Viscosity shifted the bisection point across both movement types (left); however, precision was influenced by movement, but only when no viscosity existed.

Drift diffusion modeling

The results of this Experiment appeared to support the hypothesis that increasing viscosity while judging an auditory interval led to a shorter perception of that interval. However, as stated in the Introduction, a shift resulting from increased viscosity could have either altered perception or biased subjects to classify intervals as 'short'; both outcomes could explain our results, as our task inherently involves a directional judgment (Yates et al., 2012; Schneider and Komlos, 2008). To further tease apart these two possibilities, we decomposed choice and RT data using a drift diffusion model (DDM) of perception and decision making. We employed hierarchical DDM (HDDM; Wiecki et al., 2013) in order to constrain fitted parameters for individual subjects by the group mean (see Materials and methods). Under this framework, evidence is accumulated over time towards a 'long' or 'short' decision boundary. A shift in the drift rate towards one of these boundaries is interpreted as evidence in favor of a shift in the perceptual evidence, whereas a change in the threshold boundary could be interpreted as a change in the decision layer (Voss et al., 2004; Hagura et al., 2017; Bogacz et al., 2006).

In constructing our model, we relied on a previously-formulated DDM for describing behavior in temporal categorization tasks (Balci and Simen, 2014). Under this framework, categorization is described as a two-stage process, in which elapsed time is measured during an initial processing stage, which then sets the parameters for a second-stage decision process. Specifically, the first stage is conceived as a single drift process with a variable drift rate, akin to pacemaker-accumulator models of time perception (Allman et al., 2014). At interval offset, the second-stage process begins, in which another drift process is engaged towards either an upper or lower decision boundary for classifying intervals as 'long' or 'short' (Wiener et al., 2018). Critically, the starting point (z) and drift rate (v) of the second stage process are determined by the accumulated value at the end of the first stage process; shorter or longer intervals in the stimulus set lead to starting points closer to the short or long boundaries, respectively and faster

drift rates. In this way, the starting point and drift rate are linked, with both parameters set by the perception of the timed interval.

However, the low trial count in our study precluded us from building a DDM that could simultaneously account for both increasing duration and viscosity. To address this, and ensure that our findings accorded with the predictions of the Balci and Simen, 2014 model, we constructed two separate DDMs, one for each factor, termed the Duration Model and Viscosity Model (see Materials and methods). For each model, comparisons of model complexity were conducted by comparing DIC values, as well as posterior predictive checks. For the Duration Model, we initially observed that a model which included all four DDM parameters varying with duration (v, a, t, z) was best able to account for subject data [Full model DIC = 6967.01; v, a, t model DIC = 7350.09; v, a model DIC = 8076.33; v model DIC = 9514.65; empty model DIC = 15677.96]. Posterior predictive checks of the data additionally demonstrated that the Duration Model was able to produce a similar pattern to subject data for both choice and RT (Figure 4—figure supplement 2A). For individual parameters, we additionally observed patterns that matched those reported by Balci and Simen (2014; see also Wiener et al., 2018 for a replication of these patterns). These included a change in drift rate from the short to long duration boundary with increasing duration length and a linear increase in the starting point from the short to long. Additional patterns from Balci and Simen (2014) were also observed, including U-shape and inverted U-shape patterns for threshold and non-decision time, respectively (Figure 4—figure supplement 2B). Finally, we observed the predicted linkage between starting point and drift rate, with a strong correlation between them [Pearson $r = 0.664$, $p < 0.001$; Spearman $r = 0.618$, $p < 0.001$] (Figure 4—figure supplement 2C).

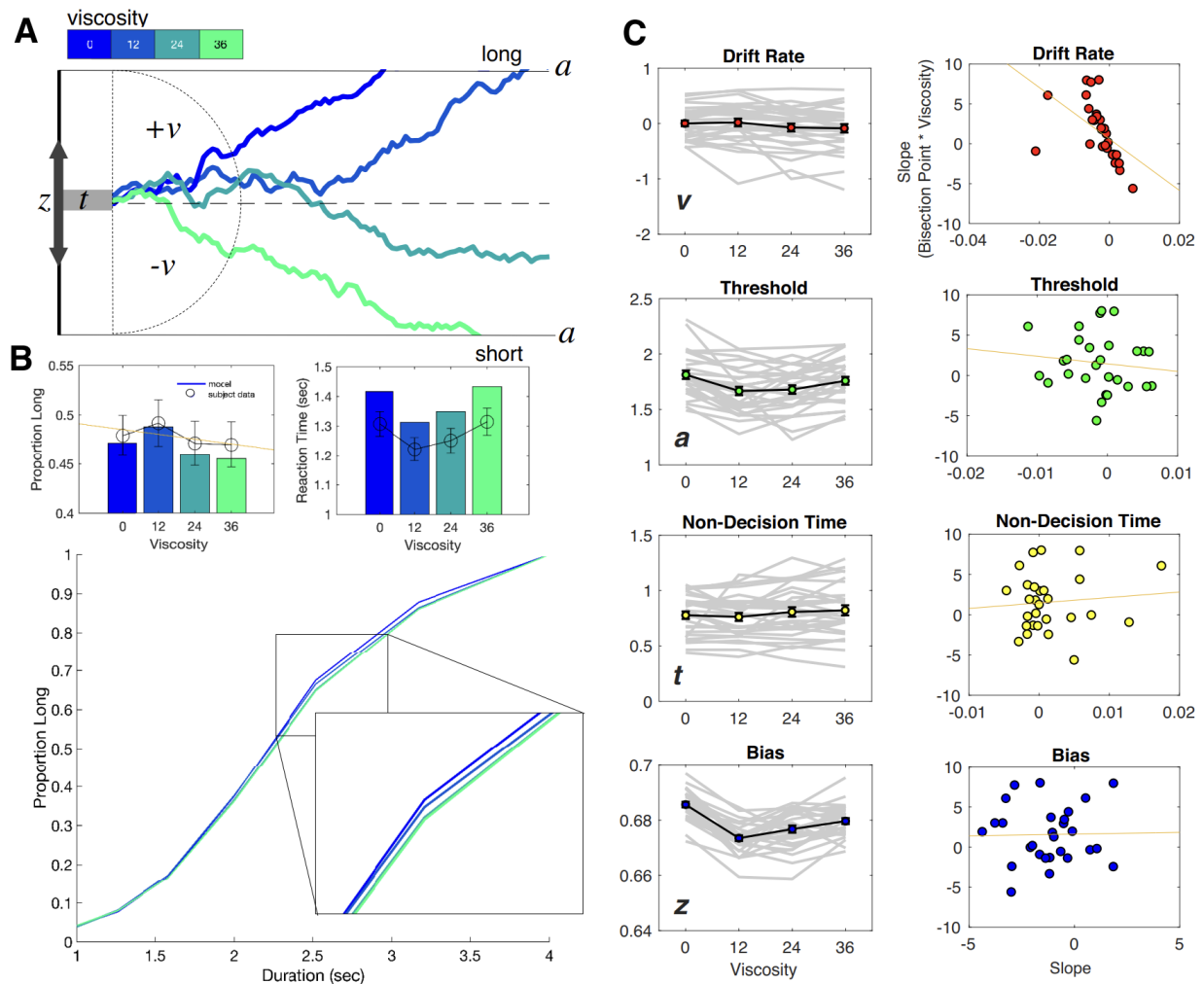


Figure 4. Drift diffusion modeling of categorization performance and viscosity. (A) Example Viscosity DDM model, in which evidence is accumulated to one of two decision bounds ('long' and 'short'), separated by a . Evidence accumulation drifts at particular rate (v) that can be positive or negative, depending on the direction of the drift to a particular boundary. The drift rate is additionally delayed by non-decision time (t) and may be biased toward one of the boundaries by a certain amount (z). Viscosity was specifically found to influence the drift rate, in which higher viscosities were associated with a shift in drift from the long to short decision boundary (presented traces represent example simulations). (B) Top Panels: Posterior predictive checks for the Viscosity Model, displaying simulated data (bars) against average subject data for choice (left) and reaction time (right). Bottom Panel: Psychometric curves from simulations of the 'Full' Model, combining Viscosity and Duration; inset displays a shift in

Viscosity in choosing ‘long’ (C) Fitted Viscosity Model results for all four parameters (left panels), showing that viscosity linearly shifted the drift rate, but also modulated threshold and bias parameters in a nonlinear (stepwise) manner. Right panels demonstrate the correlation between the slope of the viscosity effect on each parameter and the slope of the viscosity effect on behavior; only drift rate exhibited a significant correlation (see also Table 1 for Fisher Z comparisons between correlations). The online version of this article includes the following figure supplement(s) for figure 4:

Figure supplement 1. Comparison of hierarchical and non-hierarchical fits for Experiment 1.

Figure supplement 2. Parameters and simulations of the Duration Model for Experiment 1.

Table 1. Correlation coefficients and Fisher Z comparisons between fitted parameters and behavioral effects.

	Experiment 1 - Correlation with Viscosity Effect				Experiment 2 - Correlation with Viscosity Effect			
	drift (v)	threshold (a)	starting point (z)	non decision time (t)		offset (b)	production (p)	measurement (m)
Pearson	*0.5132	0.1211	0.0196	0.0926	Pearson	*0.7332	0.0626	0.0509
Spearman	*0.7865	0.168	0.0252	0.0733	Spearman	*0.709	-0.1022	-0.0299
Fisher Z compare Pearson with drift		-3.491	-1.588	-2.424	Fisher Z compare Pearson with drift		2.508	2.545
Fisher Z compare Spearman with drift		-5.312	-3.242	-3.886	Fisher Z compare Spearman with drift		2.711	2.263

Table 1. Correlation coefficients and Fisher Z comparisons between fitted parameters and behavioral effects.

For the Viscosity Model, we initially observed that having all four parameters vary by viscosity was not warranted; critically, this was driven by inclusion of the starting point, suggesting that changes in the starting point with viscosity did not improve the model fit [Full model DIC = 15245.36; v,a,t model DIC = 15213.62; v,a model DIC = 15747.6833; v model DIC = 15792.24; empty model DIC = 15678]. However, given our a-priori assumption that all four parameters could vary, and the inclusion of the starting point in the Balci and Simen, 2014 model, we report results here for the full model, noting the inclusion of the starting point does

not change these findings. In our analysis of the fitted DDM parameters for the Viscosity Model, we observed first a significant shift in the drift rate (v) with increases in viscosity [$F(3,81)=4.562$, $p=0.005$, $\eta^2_p = 0.145$]; this shift was notably linear in nature, with the drift rate shifting to the 'short' duration boundary with higher viscosities [$F(1,27)=7.866$, $p = 0.009$, $\eta^2_p = 0.226$]. Further analyses also revealed significant effects of viscosity on the threshold (a) [$F(3,81)=12.356$, $p < 0.001$, $\eta^2_p = 0.314$] and starting point (z) [$F(3,81)=43.73$, $p < 0.001$, $\eta^2_p = 0.618$], but no effect on the non-decision time [$F(3,81)=2.257$, $p = 0.088$] (Figure 4b). In both cases for the threshold and starting point, the dominant pattern was for these values to drop for viscosities above zero, but show little variation beyond that. We additionally note that this pattern can explain the RT findings observed with viscosity; specifically, a lower threshold should be associated with faster RTs. With higher viscosity, and so higher effort, subjects may have placed greater emphasis on speed for their responses, and so lowered the necessary threshold for evidence (Burk et al., 2014; Hagura et al., 2017). However, we note that this effect dropped off with higher viscosities, further suggesting that the greater effort needed to employ this strategy reduced its effectiveness.

Given the linear pattern observed for changes in the drift rate, we further explored whether this parameter could exclusively explain the shift in the BP. To test this, we calculated the slope of a linear regression for each parameter against viscosity for each subject, and correlated these with the slope values for BP against viscosity. Here, the only significant correlation observed was for the drift rate [Pearson $r = -0.5132$, $p = 0.0052$; Spearman $r = -0.7865$, $p < 0.001$], and not for any other parameter (all $p > 0.05$). A Fisher's Z-test comparing this correlation confirmed that it was significantly greater than for all other parameters (see Table 1). We additionally confirmed this correlation was correct when using a non-hierarchical method for fitting the Viscosity Model, to confirm that the results were not driven by potential shrinkage resulting from the hierarchical method (Figure 4—figure supplement 1; Katahira, 2016).

Experiment 2 - temporal reproduction

The results of Experiment 1 demonstrated that increased resistive force while subjects made temporal judgments about auditory durations led to shorter reported lengths of those durations. Computational modeling using a DDM further suggested that this shift was due to viscosity altering the perceived duration, rather than altering decision bias. However, in this experiment, decision-making and perception are intertwined, such that subjects must simultaneously measure the interval duration while classifying it. Indeed, previous research has suggested that, once the categorical boundary (here, the BP) has been crossed, subjects may stop accumulating temporal information altogether (Wiener and Thompson, 2015).

To further disentangle whether viscosity impacts perception or decision layers, we had a new set of subjects ($n = 18$) perform a temporal reproduction task, in which they moved the robotic arm while listening to auditory tone intervals and encoding their duration (Figure 5). As a critical difference from Experiment 1, in Experiment 2 subjects were required to move throughout the interval – any halts in movement were penalized by re-starting the trial. This was done following our observation in Experiment one that some subjects chose to move very little. Following the encoding phase, the arm was locked in place and subjects reproduced the duration via a button-press attached to the handle (see Materials and methods). Viscosity was again randomized across the same four levels during the encoding phase; in this way, the impact of resistive force was applied only while subjects were actively perceiving duration, without any deliberative process.

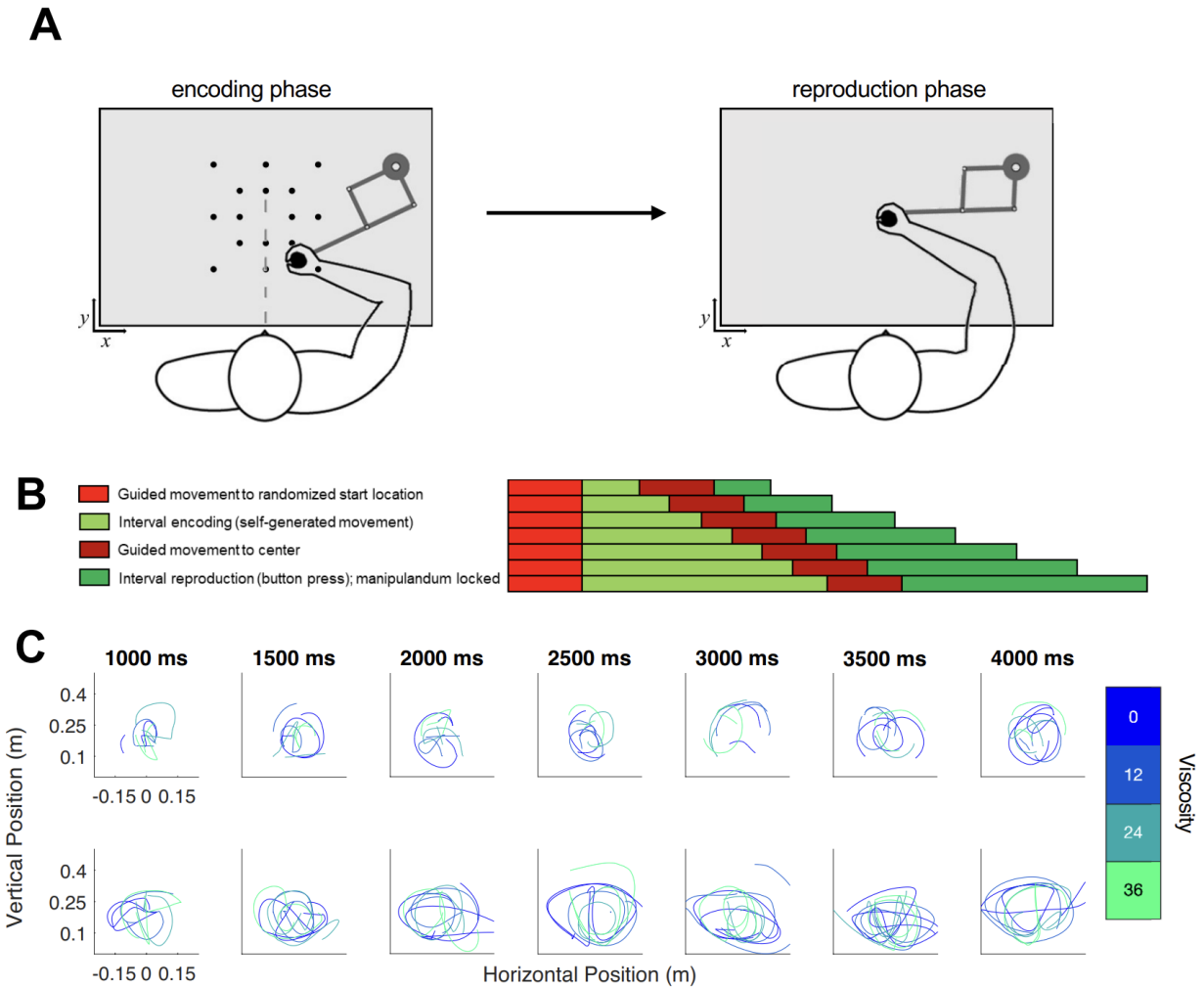


Figure 5. Task schematic of Experiment 2. (A) Participants began each trial at a randomized start location and were required to initiate movement in order for the test duration to play (encoding phase). Unlike Experiment 1, the desired viscosity was applied immediately rather than in a ramping fashion. Then, the handle was brought to a central location where participants reproduced the duration by holding and releasing a button attached to the handle. (B) Timeline for each of the seven tested intervals. (C) As in Experiment 1, each row displays sample trajectories from two subjects for the seven possible tone durations, with separate lines indicating different viscosities.

We initially confirmed again that our viscosity manipulation was effective, with reduced movement distance [$F(3,51)=149.82$, $p < 0.001$, $\eta^2_p = 0.898$] and increased force [$F(3,51)=114.84$, $p < 0.001$, $\eta^2_p = 0.871$] observed with greater viscosities (Figure 1—figure supplement 1B). For behavioral results, we initially measured the reproduced durations (t_p), finding both a main effect of viscosity [$F(3,51)=5.5$, $p = 0.002$, $\eta^2_p = 0.244$] and an interaction with the presented duration [$F(3,51) = 1.814$, $p = 0.023$, $\eta^2_p = 0.096$]. No impact on the variance of reproduced estimates was observed, with the CV remaining stable across all viscosities [$F(3,51)=0.691$, $p = 0.562$; $BF_{10}=0.016$] (Figure 1— figure supplement 1B). More specifically, we observed that reproduced durations generally were overestimated compared to the presented sample durations (t_s), and this effect was quantified by measuring the offset for each reproduced duration compared to the presented one, also known as the Constant Error; here, we additionally observed an effect of viscosity, with less overestimation with increasing viscosity [$F(3,51)=5.5$, $p = 0.002$, $\eta^2_p = 0.244$] (Figure 2B). We additionally observed an increase in the so-called central tendency effect, in which reproduced durations gravitate to the mean of the stimulus set, with greater viscosities; this effect was quantified by a change in slope values of a simple linear regression [$F(3,51)=3.473$, $p = 0.023$, $\eta^2_p = 0.17$].

Influence of movement parameters

Similar to Experiment 1, we examined the potential influence of individual differences in movement parameters on the experimental findings. Unlike Experiment 1, subjects were required to continue moving at all times during the interval, and so we predicted less heterogeneity in subject performance. As expected, we observed a close link between movement distance and force exerted, yet with a narrower range for each than in Experiment 1 (Figure 1—figure supplement 1B). Unlike Experiment 1, we found no correlation between the effects of viscosity on Movement Distance and Force [Pearson $r = -0.16$, $p = 0.52$; Spearman $r = -0.14$, $p = 0.55$], suggesting the correlation observed in Experiment 1 was primarily driven by some subjects moving very little. Additionally, we observed no between-subject correlation

between the effects of viscosity on movement distance and duration reproduction [Pearson $r = 0.07$, $p=0.75$; Spearman $r = 0.19$, $p=0.44$], nor on force and duration reproduction [Pearson $r = 0.008$, $p=0.97$; Spearman $r = -0.23$, $p=0.34$] (Figure 1—figure supplement 1B).

Bayesian observer model

The results of Experiment 2 revealed that, with increasing viscosity while encoding a time interval, the reproduced interval was increasingly, relatively, shorter in length. Again, this finding is consistent with reduced movement altering the perception of temporal intervals. We note that the temporal reproduction task as designed does not share the overlap with decision-making as in the temporal categorization task, as viscosity was only manipulated while subjects estimated the interval, and was not included during reproduction. However, we also note that the behavioral data alone are somewhat ambiguous to how viscosity impacts time estimation, as we observed both a shift in time intervals, as well as an increase in central tendency with greater viscosities. Changes in central tendency may be ascribed to a shift in uncertainty while estimating intervals, and although the CV did not change across viscosities, it remains possible that viscosity led to greater uncertainty, which would explain the observed shifts.

To tease these two possibilities apart, we employed a Bayesian Observer-Actor Model previously described by Remington and colleagues (Remington et al., 2018; Jazayeri and Shadlen, 2010) (see Materials and methods). In this model, sample durations (t_s) are inferred as draws from noisy measurement distributions (t_m) that scale in width according to the length of the presented interval. These measurements, when perceived, may be offset from veridical estimates as a result of perceptual bias or other outside forces (b). Due to the noise in the measurement process, the brain combines the perceived measurement with the prior distribution of presented intervals in a statistically optimal manner to produce a posterior estimate of time. The mean of the posterior distribution is then, in turn, used to guide the reproduced interval (t_p), corrupted by production noise (p) (Figure 6a). The resulting fits to this model thus produce an estimate of the measurement noise (m), the production noise (p), and

the offset shift in perceived duration (b). Note that the offset term is also similar to that employed for other reproduction tasks as a shift parameter (Petzschner and Glasauer, 2011).

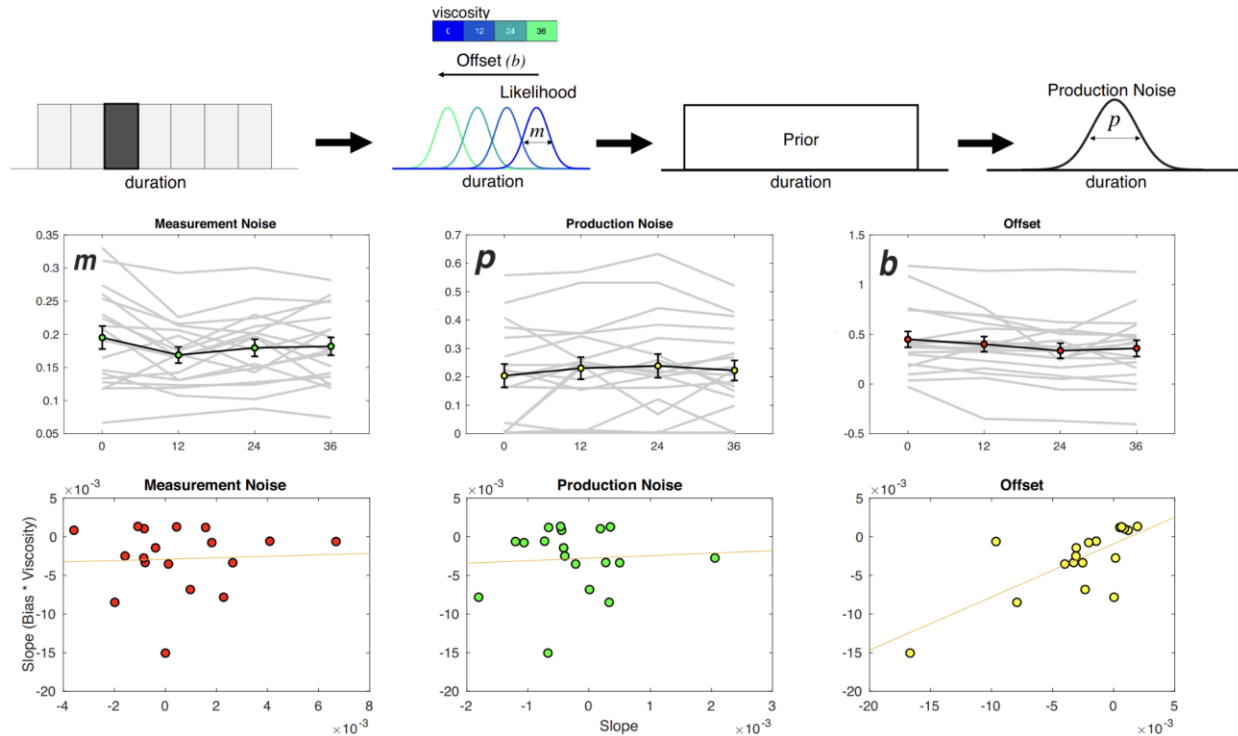


Figure 6. Viscosity shifts time reproduction. Top: Bayesian Observer Model. On a given trial, a presented duration is drawn from a likelihood distribution with scalar variance leading to a measurement estimate (m) that is shifted by an offset parameter (b). The measurement estimate is combined with a uniform prior distribution of presented durations, and then finally affected by production noise (p). Viscosity was found to specifically shift b in a linear manner, with greater viscosities associated with shorter perceived durations. Middle panels: Fitted results for all three parameters, demonstrating a linear effect of offset, no effect of measurement noise, and a nonlinear (stepwise) shift in production noise with greater viscosities. Bottom panels display correlations with the behavioral effect of viscosity; only the offset parameters exhibited a significant effect (see Table 1 for Fisher Z comparisons). Right panel was additionally significant after outlier removal.

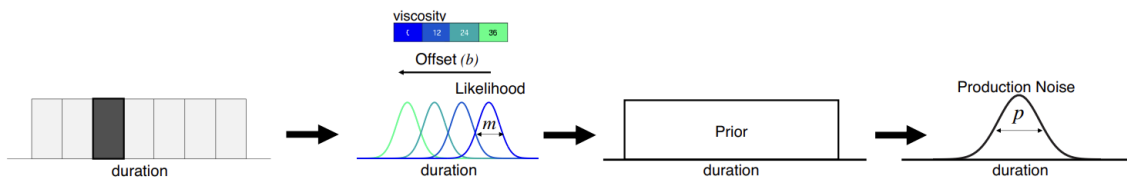
The result of the model fitting first demonstrated a significant effect on the width of the production noise (p) [$F(3,51)=3.548$, $p = 0.021$, $\eta^2_p = 0.173$] (Figure 6b). More specifically, production noise was found to decrease with higher viscosities; however, this effect was not linear, with the only difference being for zero viscosity estimates higher than all others. We note that this effect is similar in form to the shift in the threshold parameter (a) from the Viscosity-DDM of Experiment 1, and so may reflect a change in strategy from higher viscosity. That is, in response to the greater effort during measurement, subjects attempt to compensate by increasing motor precision during production (Remington et al., 2018).

For the offset shift (b), we observed a significant effect of viscosity [$F(3,51)=3.72$, $p = 0.017$, $\eta^2_p = 0.18$] that was linear in nature, with a reduction in values with increasing viscosity. No effect of viscosity was observed on the measurement noise parameter (m) [$F(3,51)=1.212$, $p = 0.315$]. As with the DDM results of Experiment 1, we further explored whether the linear nature of the shift in b could best explain the observed underestimation of duration by calculating the slope of a regression line for each parameter against viscosity and compared that to the change in reproduced duration. Only the offset term significantly correlated with the underestimation effect [Pearson = 0.7332, $p < 0.001$; Spearman = 0.709, $p < 0.001$]. Again, a Fisher's Z-test comparing this correlation confirmed that it was significantly greater than for all other parameters (see Table 1).

In order to extend the modeling results further, we sought to compare these findings to an alternative version of the Bayesian model. We therefore constructed a second model in which the offset term (b) was moved from occurring at the measurement stage to the production stage (Figure 7A). This second model, termed the Viscosity Production Model, was fit to subject data and compared to the first model, termed the Viscosity Perception Model. For comparison, we conducted predictive checks by simulating data from both models and plotting these simulations against the observed subject data (Figure 7B). Here, we observed that while the Viscosity Perception Model provided a good fit and description of the data, including a replication of the

linear effect of viscosity on constant error, the Viscosity Production Model failed to do so. This observation was confirmed by comparing Negative Log-Likelihood estimates of model fits across subjects and viscosities, in which the Perception Model provided a significantly better fit [$F(1,17)=21.686$, $p<0.001$, $\eta^2_p = 0.561$] (Figure 7). We further note that, for the Production Model, the effect of viscosity was not significant [$F(3,51)=0.871$, $p=0.462$], suggesting that the model was not simply shifted from the true response. Notably, the Production Model was still able to capture the effect of production noise we observed in the Perception Model [$F(1,17)=3.211$, $p=0.031$, $\eta^2_p = 0.159$].

A Viscosity Percept Model



Viscosity Production Model

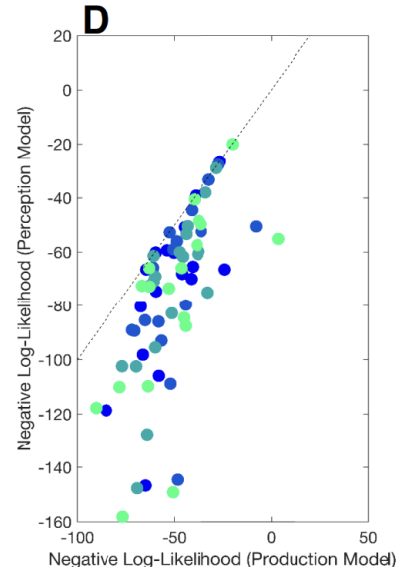
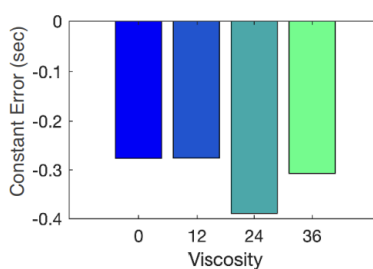
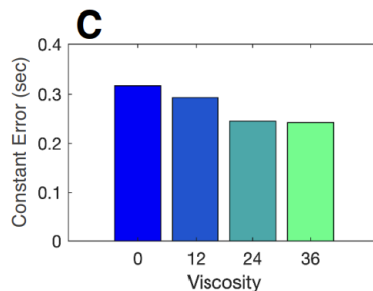
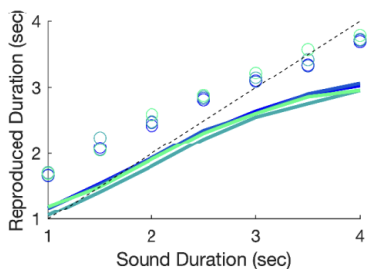
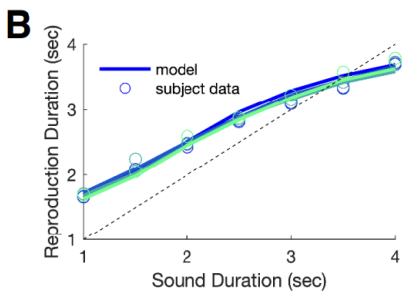
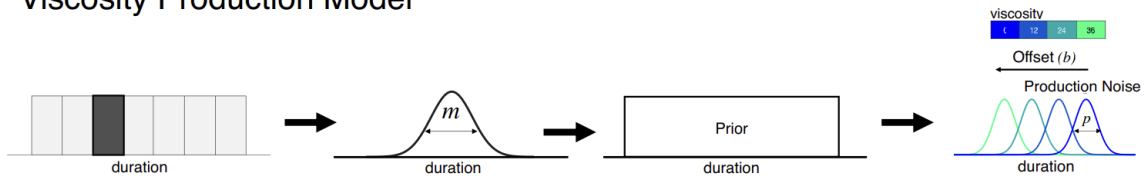


Figure 7. Bayesian observer model of reproduction performance and viscosity. (A) Schematics for separate Bayesian models, in which the offset term could occur at either measurement level (Perception Model) or the production level (Production Model). (B) Predictive checks for both models, in which model simulations are presented with average subject data for Perception Model (top) and Production Model (bottom). (C) Average Constant Error for Perception (top) and Production (bottom) model simulations. (D) Comparison of Negative Log-Likelihood values for model fits for each model; individual data points represent single subjects, with each color representing a different viscosity. Dashed line represents the identity.

Discussion

The above experiments demonstrate that systematically impeding movement during interval timing leads to a subsequent compression of perceived duration. These findings complement previous work showing that time perception is highly sensitive to movement (Yon et al., 2017; Yokosaka et al., 2015; Tomassini and Morrone, 2016), and here we confirm a case in which movement parameters (e.g., length and duration) did not have to be self-modulated to induce these distortions. The movement restrictions we implemented (i.e. moving in environments with different manipulations of viscosity) tended to shift the BP later in time in a temporal categorization task, and subsequently shortened perceived intervals in a temporal reproduction task.

In the temporal categorization task, we found that increased viscosity, on average, shifted the BP such that subjects responded 'long' less often. We then applied a drift-diffusion model to isolate the cognitive mechanisms contributing to this effect (i.e. whether it was a function of decision bias, speed-accuracy trade-off calibration, non-decision time, or the rate of evidence accumulation; Ratcliff, 1978). The only significant contributor was the drift rate parameter, which linearly shifted from the 'long' to the 'short' boundary with increasing viscosity. While this was evidence for a purely perceptual effect of viscosity on perceived time, we further

investigated this effect by administering a temporal reproduction task in Experiment 2. Eliminating the decision process ensured that recorded responses were more representative of timing distortions via perceptual modulation. Here, participants made temporal estimations during movement, and reproduced these via button press. Although in the temporal categorization task the degree of movement between participants was self-selected and highly variable, we attempted to reduce this variability by requiring participants to move continuously during trials in the temporal reproduction task. We also controlled for performance variability due to familiarization by including a brief training session. Participants exhibited an overestimation bias when reproducing the interval duration, a result previously shown in motor reproduction of auditory intervals (Shi et al., 2013). However, the degree of overestimation decreased as a function of viscosity, confirming the compression effect seen in the temporal categorization task. Using a Bayesian observer model (Jazayeri and Shadlen, 2010; Remington et al., 2018), we observed a linear shift in perceptual bias as a function of viscosity, further supporting a purely perceptual effect of movement slowing on timing.

The results between experiments converge on the finding that viscosity manipulation leads to interval underestimation (reflected in the bias parameters). Further, timing precision was generally unaffected by our manipulations. In the temporal categorization task, the CV remained constant across viscosities; the only notable CV effect was revealed by the median split analysis, in which trials with greater movement led to greater precision for the zero viscosity condition. This was in agreement with our previous study demonstrating a movement-related enhancement in temporal precision estimates (Wiener et al., 2019), and suggests that free movement can improve timing precision only in unrestricted movement environments. The temporal reproduction task also showed that viscosity did not affect the variability of estimation (CV), but interestingly, may have been associated with greater uncertainty as indicated by increased central tendency of reproduction slopes.

In addition to the paradigm difference in Experiments 1 and 2, it is worthwhile to consider the methodological differences that may have influenced these results. As mentioned above, in our first experiment we allowed movement, while in the second experiment we required it. Additionally, movement in the temporal categorization task had utilitarian value; participants could strategically approach candidate targets, and thus movement offered the potential to improve performance by shortening RTs. Movement in the temporal reproduction task did not provide this decision-making advantage, but notably the perceptual biases due to viscosity maintained the same directionality across experiments. That is, in response to viscosity, the BP parameter in Experiment one and the perceptual bias parameter in Experiment 2 shifted upwards and downwards respectively, in accordance with temporal compression. This suggests that movement influenced similar temporal estimation mechanisms, and despite methodological differences, the biasing effect of viscous environments was robust under different task demands. One additional note regarding this work is that subjects were not required to time their movements but were rather using their movements for timing. We believe the distinction here is important, as the ancillary movement patterns nevertheless influenced the perceived timing.

Our results parallel prior work investigating temporal distortions as a function of movement parameters. (Press et al., 2014) presented tactile stimulation to participants' fingers during movement or while stationary as they viewed congruent or incongruent hand avatars displayed on a screen. The duration of the tactile stimulus was perceived as longer when the avatar was congruent to concurrent movement. (Yon et al., 2017) similarly found that when participants executed finger movements of a pre-specified duration and listened to an auditory stimulus with an independently selected duration, judgments were biased towards the duration of the movement. They followed this with a separate experiment focused on manipulating movement distance as a proxy for movement duration (with the knowledge that farther reaches typically take longer); participants reached towards targets along a flat workspace with variable distances while a concurrent auditory duration was presented. Durations presented during 'far'

reaches were again perceived as longer. This bears similarity to our experiments here, with a few key distinctions: in our experiments, movements were scaled exclusively in the spatial, but not temporal domain as a function of viscosity (i.e. movement distance, but not movement duration, scaled with viscosity). Additionally, the Yon experiments relied on volitional modulation for task success (e.g. being trained to make 'short' and 'long' movements or reach 'near' and 'far'). Our manipulation affected movement distance without any change in task demands; that is, the manipulated sensory feedback (via the somatosensory system) offered no explicit benefit or detriment to completing the task. Participants certainly reacted to these perturbations by increasing applied force, but self-modulation and monitoring in response to the manipulation was not required as in Yon et al., 2017. We believe this is a critical insight given by our study; even though participants knew that demands did not change with viscosity, the manipulation still induced temporal biases – presumably without conscious awareness. Taken together, these findings suggest complementary mechanisms of temporal biasing by movement distance and duration that are often conflated due to distance-duration correlations.

In contrast, some prior accounts do not align with our results. For example, Yokosaka et al., 2015 found that visual intervals demarcated by pairs of visual flashes were compressed during fast hand movement, whereas in our experiment we show that slowing down movement leads to compression. Additionally, Tomassini and colleagues (Tomassini et al., 2014) reported that tactile intervals were compressed during hand movement. Considering these examples, a crucial note—as highlighted in Iwasaki et al., 2017—is that many of the distortive effects of movement can be linked to whether an interval is filled or unfilled. Indeed, while we utilized filled auditory intervals in our tasks, the studies with contrasting effects utilized unfilled intervals. Also of interest is the type of movement in the listed studies and the interval ranges used. Movements were typically stereotyped across trials, and intervals were tested in the subsecond range. Here, we allowed participants to move freely along a two-dimensional plane and there were considerable individual differences in selected trajectories. Most notably, it was the

externally imposed restriction of movement that turned out to be more influential on temporal perception than self-modulated movement characteristics.

In future movement-timing experiments it may be fitting to look beyond simple movement parameters (e.g. speed and distance) and focus on higher-order parameters such as biological versus non-biological motion. Specialized detection systems in the brain can identify movement from other organisms that adhere to physical principles such as natural acceleration and deceleration patterns, and are studied in laboratories from using simple stimuli (e.g. moving dot displays; Gavazzi et al., 2013) to complex light-point representations of locomotion (Wang and Jiang, 2012). When timing the duration of a dot moving across a screen with different movement profiles, biological motion (compared to constant motion) is timed more precisely for sub- and supra-second intervals, and more accurately for sub-second intervals (Gavazzi et al., 2013). Wang and Jiang, 2012 found that the perceived duration of a human light-point display was expanded compared to a static or nonbiological motion display, and this effect persisted when the dot positions were scrambled but retained local kinematics. However, studying motor production of biological motion during timing is a fairly new concept. Carlini and French, 2014 asked participants to time a dot stimulus moving across a screen that they either tracked with their finger, or viewed passively. Hand tracking overall improved accuracy and precision, but the improvement occurred irrespective of the movement type (biological motion, constant velocity, or sharp 'triangular' velocity profile). Additionally, biological motion was timed most accurately and precisely with or without manual tracking. This highlights a benefit of concurrent movement that can increase the accuracy of non-biological motion timing to biological motion levels. A natural question that follows concerns the degree to which these different motion types are biased from external factors. For example, would the compressing effect of viscosity occur more strongly for non-biological motion because it is more susceptible to motor influences? If we were to administer a similar manual tracking task, we predict that this would be the case. This design would also allow us to examine the separate contributions of force and movement distance; to

examine movement distance we would scale the cursor speed down with viscosity (thereby requiring the same amount of cumulative force between viscosities), and to examine force we would keep the speed constant (requiring a compensatory force increase with viscosity).

This novel contribution to the existing body of research highlights the importance of sensory feedback in timing, whereas the study of movement-induced time distortions has focused primarily on feedforward effects. These complementary accounts enrich the current understanding of the coupling of movement and time perception, and support the longstanding notion that interval timing in the brain utilizes multiple streams of sensory information and distributed timing circuits to form a unified percept of duration (Chen and Vroomen, 2013; Bausenhart et al., 2014; Wiener et al., 2011). Understanding the integration of these signals is an important problem in modern neuroscience, and here we have presented a strong case for greater investigation into the role of movement perturbations in time perception. More specifically, they point to an intrinsic role of the motor system in time perception. As described above, previous research has shown motor system involvement in time perception, even when no timed motor response is required (Nani et al., 2019). Further, temporal categorization, as employed here has been linked to motor system processing and neural populations within the supplementary motor area (SMA), a region highly implicated in timing (Schwartz et al., 2012; Mendoza et al., 2018; Méndez et al., 2014).

Most saliently, our results align with A Theory of Magnitude (ATOM), an account outlining common neural circuitry between spatial, temporal, and numerosity representations in the brain (Walsh, 2003). The manipulation we introduced scaled spatial characteristics of movement, and subsequently led to a scaling down of perceived duration. A relevant consideration here is that viscosity was introduced via sensorimotor channels but had a cross-modal effect on auditory timing. This highlights an issue not originally included in ATOM: the role of simultaneous temporal measurements from different sensory channels. Our results suggest that the two channels of temporal processing were not redundant; if this had been the

case, there would have been no effect of movement on the separate auditory estimate. We propose that these effects can be approached from a perspective of optimal cue combination (Ball et al., 2017). In a previous study (Wiener et al., 2019), we found that movement (versus no movement) enhanced temporal precision. Combined with the knowledge that movement can also bias timing, we suggest that noisy auditory estimates in our experiments reaped a benefit from integrating motor information with higher precision, at the cost of a slight bias. To more thoroughly understand how motor and sensory time estimates interact, it is essential to examine the weighting of separate sensory pathways according to their usefulness and their reliability. Although the current study is not equipped to dissociate motor and auditory contributions, we strongly recommend this principle as a productive area of focus for future work.

Beyond understanding basic mechanisms of temporal processing and movement, these approaches may be of interest in order to study clinical disorders for which timing and movement are disrupted. Notable work in recent years has strongly suggested that motor control is an extension of ongoing cognitive computations (Lepora and Pezzulo, 2015; Resulaj et al., 2009), and adopting an integrated view of cognition-action pathways is a promising avenue for understanding these disorders and developing therapies that exploit these links. For example, in the case of Parkinson's (PD) and Huntington's Diseases (HD), core timing networks in the brain overlap substantially with the motor circuitry targeted by neural degeneration, such as the basal ganglia (Obeso et al., 2000; Obeso et al., 2014; Browne et al., 1997). Motor deficits in these diseases are often accompanied by timing deficits (Avanzino et al., 2016) and other cognitive abnormalities (Robbins and Cools, 2014; Paulsen, 2011). The shared neural circuitry combined with these parallel deficits provide a basis for incorporating movement into cognitive training and vice versa.

In contrast, psychiatric and neurodevelopmental disorders are usually discussed in terms of cognitive deficits despite exhibiting motor idiosyncrasies. Although embodied cognition has gained traction in basic science research, there are fewer approaches in clinical research

that consider cognitive and motor symptoms in relation to one another. One example is attention deficit hyperactivity disorder (ADHD). The excessive motoric activity (i.e. hyperactivity) associated with the disorder is typically seen as disruptive, but interestingly, some studies have shown that it can boost cognitive control performance (Rapport et al., 2009; Hartanto et al., 2016). In light of the timing deficits present in ADHD (Plummer and Humphrey, 2009), it would be interesting to explore the extent movement can provide a similar benefit to timing performance. The coupling of timing and motor functions taken together with the supramodal nature of core timing circuits provides an excellent opportunity to probe cognition-action pathways in various clinical disorders. On the one hand, movement can sharpen certain perceptual and cognitive processes, and on the other hand, it can introduce biasing effects on timing and on other perceptual judgments (Moher and Song, 2014), including when movement perturbations are applied (Hagura et al., 2017). Therefore, further investigation is warranted to better understand how these effects can be exploited to improve outcomes for patients.

In summary, we tested participants' ability to time intervals while moving, and in two separate timing paradigms demonstrated that imposing restrictions on movement subsequently shortened perceived time. Computational modeling confirmed that these effects arose from perceptual differences rather than downstream cognitive processes. The influence of motor activity on sensory processing is well studied—motor activity can modulate sensory processing across modalities, as early as in primary sensory cortices (for review, see Parker et al., 2020). For example, locomotion can modulate gain in rodent visual and auditory cortices (Niell and Stryker, 2010; Zhou et al., 2014), and in humans, orientation change detection is improved when preparing to make a grasping motion aligned with the original orientation (Gutteling et al., 2011). Recent reports have shown that timing, through a neurally distributed system, is also modulated by and can even be improved by movement (Wiener et al., 2019; Carlini and French, 2014; Manning and Schutz, 2013). Our work confirms that time is subject to distortion by externally imposed movement constraints and allowances, at least in the auditory modality and

within the suprasedond range. It is important to note that timing distortions can be modality-specific (Buetti, 2011), and as stated above, differ when intervals are filled versus unfilled (Iwasaki et al., 2017). These are natural considerations regarding our results, and could form the basis for future work to investigate different modalities, temporal ranges, and interval presentation styles. Another consideration is that in our experiments, viscosity was fixed throughout each trial; in followup experiments, it would be interesting to calibrate the nature and degree of movement perturbations to observe the resulting effects on timing. For example, experimenters could introduce dynamic perturbations or alter visual feedback much like in motor adaptation experiments (Shadmehr and Mussa-Ivaldi, 1994; Krakauer et al., 2000; Alhussein et al., 2019; McKenna et al., 2017; Zhou et al., 2017).

Materials and methods

Participants

A total of 28 participants took part in Experiment 1 (18 female, 10 male, M age = 23.5 (7.0)) and 18 separate participants took part in Experiment 2 (7 female, 11 male, M age = 21.5 (4.1)) for \$15 per hour in gift card credit. These sample sizes were chosen to accord with our previous report (Wiener et al., 2019). All participants were right-handed as measured by the Edinburgh Handedness Inventory (Oldfield, 1971). All protocols were approved by the Institutional Review Board at the University of California, Davis.

Apparatus

Both experiments utilized a robotic arm manipulandum (KINARM End-Point Lab, BKIN Technologies; Nguyen et al., 2019; Hosseini et al., 2017). Here, the participants manipulated the right arm on a planar workspace to perform the tasks and were blocked from viewing their arm directly by a horizontal screen display. A downward-facing LCD monitor reflected by an upward-facing mirror allowed viewing of experiment start locations and targets, demarcated by small circles. Participants were seated in an adjustable chair so that they could comfortably view the mirrored display. In Experiment 1, a cursor on the screen projected their current arm

position during each trial, whereas in Experiment 2 no cursor was present. The manipulandum sampled motor output at 1000 Hz.

Procedure

Experiment 1

In the first experiment, participants performed an auditory temporal categorization procedure (Kopec and Brody, 2010) with intervals of 1000, 1260, 1580, 2000, 2520, 3170, and 4000 ms with a 440 Hz tone. A total of 280 trials were segmented into five blocks with the option for a short (1–2 min) break between each block. Participants were instructed to start each trial in a central target location, where the manipulandum locked the arm in place for 1000 ms. A warm-up phase began as the hold was released and the words ‘Get Ready’ were displayed on the screen. Participants were encouraged during instruction to move freely throughout the workspace during each trial, and respond as quickly and accurately as possible. During the warm-up phase, viscosity was applied in a linearly ramping fashion, reaching one of four viscosity values (0, 12, 24, or 36 Ns/m²) in 2000 ms. Simultaneously, two response targets appeared at 105° and 75°, equidistant from the starting location. Target assignment was counterbalanced between participants. Once the desired viscosity was reached, the tone began to play and participants were required to determine whether the tone was short or long compared to all tones they had heard so far (reference-free categorization) by moving the cursor to the corresponding target location on the right or left. If a response was made before the tone had elapsed, the trial was discarded and they were required to repeat the trial. No feedback was given. Viscosity and duration values were randomized across trials with equal representation in each block.

Experiment 2 (temporal reproduction)

In the second experiment, a separate group of participants performed a temporal reproduction task with tone intervals of 1000, 1500, 2000, 2500, 3000, 3500, and 4000 ms. Because the task had higher attentional demands and was more likely to cause fatigue, the 280

trials were segmented into 10 instead of five blocks. In this task, the manipulandum moved the participant's arm (1000 ms) to the one of 16 encoding start locations in a grid-like configuration, and locked in place for 1000 ms until a green 'go' cue appeared in the start location. Upon seeing the cue, participants were required to start moving. Moreover, the tone onset was contingent upon movement, and the trial was discarded and repeated if movement stopped before tone offset. After tone offset, a linearly ramping 'brake' was applied to discourage further movement. Once movement stopped, the manipulandum moved to a central location for the reproduction phase. After seeing a green cue, participants reproduced the encoded interval by holding and releasing a button attached to the manipulandum. No auditory or performance feedback was given. As in Experiment 1, duration and viscosity were randomized and equally represented in each block.

Analysis

In Experiments 1 and 2, movement distance and force measures were taken for each trial. Movement distance was defined as the summed distance traveled (point-by-point Euclidean distance between each millisecond time frame) during the stimulus tone. Force was similarly defined as the summed instantaneous force during the stimulus tone. In Experiment 1, RT was defined as the time elapsed between tone offset and reaching one of the two choice targets. Outlier trials were excluded for RT values greater than three standard deviations away from the mean of a participant's log-transformed RT distribution (Ratcliff, 1993). For each participant we plotted duration by proportion of 'long' responses. From here, we used the psignifit 4.0 software package to estimate individual BP and coefficients of variation (CV) for all four viscosity values (Schütt et al., 2016); all curves were fit with a cumulative Gumbel distribution to account for the log-spaced nature of tested intervals (Wiener et al., 2018; Wiener et al., 2019). The BP was defined as the 0.5 probability point on the psychometric function for categorizing intervals as 'long'; the CV was defined as half the difference between 0.75 and 0.25 points on the function divided by the BP.

In Experiment 2, we plotted true duration by estimated duration for each participant to find individual slope and intercept values. We also computed individual CV values for duration and viscosity conditions via the ratio of estimation standard deviation to estimated mean (Wiener et al., 2019). We excluded trials if the reproduction time fell outside three standard deviations from the mean. Additionally, we calculated the constant error, defined as the difference between the reproduced interval and the presented one.

For statistical analyses, we report the results of repeated measures ANOVAs and post-hoc t-tests where appropriate, along with effect sizes. For all correlations, we report the value of both Pearson and Spearman correlation coefficients. Additionally, for effects deemed non-significant by standard null-hypothesis statistical tests, we report Bayes Factors as calculated by the software package JASP (<http://www.jasp-stats.org>).

Drift diffusion modeling

To better dissect the results of Experiment 1, we decomposed choice and RT data using a drift diffusion model (DDM; Ratcliff, 1978; Wiecki et al., 2013; Tipples, 2015). Due to the low number of trials available per condition, we opted to use hierarchical DDM (HDDM) as employed by the HDDM package for Python (http://ski.clps.brown.edu/hddm_docs/allinone.html). In this package, individual subjects are pooled into a single aggregate, which is used to derive fitted parameters by repetitive sampling from a hypothetical posterior distribution via Markov Chain Monte Carlo (MCMC) sampling. From here, the mean overall parameters are used to constrain estimates of individual-subject estimates. HDDM has been demonstrated as effective as recovering parameters from experiments with a low number of trials (Wiecki et al., 2013).

In our approach to modeling, we opted for a DDM in which four parameters were set to vary: the threshold difference for evidence accumulation (a), the drift rate towards each boundary (v), the starting point, or bias toward a particular boundary (z), and the non-decision

time (t), accounting for remaining variance due to non-specific processes (e.g. perceptual, motor latencies). Our choice to include these four parameters was driven a priori by earlier modeling efforts for studies of timing and time perception (Tipples, 2015; Balci and Simen, 2014; Wiener et al., 2018). Nevertheless, we compared fits of models of varying complexity via the Deviance Information Criterion, in which parameters added in the following manner: null \rightarrow v \rightarrow v_a \rightarrow v_{at} \rightarrow v_{atz} . A reduction in DIC of 10 or greater was considered as evidence for a better fit. We additionally include between-trial variability in the starting point (sz) to account for trial-to-trial fluctuations.

For model construction, we relied on the model of Balci and Simen, 2014 as a guide, as in our previous work (Wiener et al., 2018; Bader et al., 2019). In this model, performance on a temporal categorization task is conceived as a two-stage process. In the first stage, evidence accumulates monotonically during the interval, serving as a measure of elapsed time. At interval offset, the second stage initiates another drift-diffusion process, in which evidence accumulates towards one of two decision bounds, associated with 'short' and 'long' categorizations. Notably, the starting point (z) of the second stage process is determined by the level of accumulation from the first stage at offset; shorter intervals lead to a starting point closer to the 'short' categorization boundary, whereas longer intervals are closer to the 'long' boundary. Further, the proximity to each of the boundaries also determines the drift-rate (z) of the second stage process, with higher drift rates for closer proximity. Thus, the drift rate and the starting point are linked in this model.

Following our previous work, we chose to model only the second-stage process. This choice comes from previous studies as well as Balci and Simen (2014; supplementary material) who demonstrated that modeling the second-stage alone is sufficient at capturing all of the predicted effects. However, in designing the model, we note that there was an insufficient number of trials to account for both duration and viscosity, as the number of trials for each combination was lower than recommended by HDDM (10). As such, in order to demonstrate

that this model could account for the behavioral data, we built two DDMS – one in which the included parameters varied as a function of duration, and one in which they varied as a function of viscosity.

Model construction was accomplished using the HDDMStimCoding class for HDDM, in which the starting point was split between both short and long response boundaries. Unlike the behavioral analysis, we included all trials here, and chose to model the probability of outliers using the `p_outlier` option, in which outliers were assumed to come from a uniform distribution at the right tail of the full RT distribution (Ratcliff and Tuerlinckx, 2002). This was done to avoid differential weighting of RTs from individual subjects in the full distribution; the probability was set to 0.05. Model sampling was conducted using 10,000 MCMC samples, with a burn-in of 1000 samples and a thinning (retention) of every 5th sample. Individual model fits were assessed by visual inspection of the chains and the `MC_err` statistic; all chains exhibited low autocorrelation levels and symmetrical traces. We additionally sampled five further chains of 5000 iterations (200 burn-in) of the ‘winning’ models and compared the Gelman-Rubin Statistic (Gelman and Rubin, 1992) revealing a value of 1.011 ± 0.082 (SD) for the Viscosity model, and 1.04 ± 0.093 (SD) for the Duration model, indicating good chain stability. In addition, we conducted posterior predictive checks for both models, in which 500 samples from the posterior distributions of each parameter were randomly drawn and used to generate a new dataset. The resulting choice and RT data were analyzed and compared to behavior for both duration and viscosity models.

Once model fits were accomplished and compared to behavioral data, we sought to demonstrate that a ‘full’ model – one in which duration and viscosity varied – could account for the behavioral findings. To accomplish this, we combined both models by first conducting a posterior predictive check for the Duration model, and then shifting each drawn sample from the posterior by an amount determined by the Viscosity model for each of the four levels of viscosity. For example, the drift rate (v) drawn from the posterior of the duration model would be

averaged with the drift rate from the Viscosity model; a new dataset would then be generated using these values. In this way, four separate datasets from the Duration model were simulated, one for each viscosity. Choice and RT data were then averaged in these datasets to see if they recapitulated the original findings.

Finally, we also performed a non-hierarchical fit to subject data. This was done to confirm that the hierarchical results and their correlation with behavior were not unduly influenced by shrinkage of parameter estimates to the group mean. To accomplish this, individual subject data were fit using the `HDDM.Optimize()` function, in which results were fit via a Maximum Likelihood procedure (Ratcliff and Tuerlinckx, 2002). Individual parameter estimates were compared to the hierarchical ones, and the same correlations with behavior were conducted. This comparison was only carried out for the Viscosity model, where correlations with behavior were conducted.

Bayesian observer model

To model data from the reproduction task, we employed a Bayesian Observer Model, as developed by Jazayeri and colleagues (Jazayeri and Shadlen, 2010; Remington et al., 2018). In this model, sensory experiences of duration are treated as noisy estimates from a Gaussian distribution with scalar variability that grows linearly with the base interval, termed the measurement noise (m). Once drawn, these estimates are combined with the prior distribution of previously-experienced intervals; in this case, the prior was modeled as a uniform distribution with an upper and lower boundary corresponding to the presented intervals in the task. The mean of the resulting posterior distribution of an interval is thus drawn to the mean of the prior, thus accounting for the central tendency effect observed. Further, this effect also accounts for a trade-off in the precision of estimates; increased reliance on the prior, while increasing bias to the mean, also reduces variability, thus decreasing the CV (Cicchini et al., 2012). Following the posterior estimate, the produced movement is additionally corrupted by movement noise (p), again drawn from a Gaussian distribution. As an additional parameter, measurement bias is

also included (b), also termed the estimation 'offset' (Remington et al., 2018), in which the noisy estimate is shifted away from the true duration. Note here that b is specifically included as a shift in perception, rather than production bias, and so we refer to this as the Perception Model.

We additionally constructed a second, alternative version of this model, in which the offset parameter was instead shifted to the production stage. Specifically, the offset term was changed in this model to be added during production, following movement noise, referred to as the Production Model. Model parameters (m, p, b) for each model were fit by minimizing the negative log-likelihood of individual subjects' single trial responses, using modified code provided at (<https://jazlab.org/resources/>). Minimization was accomplished using the *fminsearch* function for Matlab, using numerical integration over the posterior distribution. Model fits were repeated using different initialization values and a fitting maximum of 3000 iterations; inspection of fitted parameters indicated good convergence of results. Model comparison was conducted by comparing negative log-likelihood values across each of the four viscosity conditions.

Lastly, we conducted predictive checks by taking the average parameter estimates across subjects and simulating two datasets (40 trials per condition). These datasets were then analyzed in a similar manner to the behavioral data and compared to average subject data. Separate simulations were conducted for the Perception and Production Models.

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Author contributions

Rose De Kock, Conceptualization, Data curation, Formal analysis, Investigation, Visualization, Writing - original draft; Weiwei Zhou, Data curation, Formal analysis, Investigation, Methodology; Wilsaan M Joiner, Resources, Software, Supervision, Funding acquisition, Methodology, Project administration, Writing - review and editing; Martin Wiener,

Conceptualization, Data curation, Formal analysis, Supervision, Funding acquisition, Validation, Investigation, Visualization, Methodology, Writing - original draft, Project administration, Writing - review and editing

Ethics Human subjects:

Informed consent was obtained from all subjects. All protocols were approved by the Institutional Review Board at the University of California, Davis (IRB Protocol # 1336438-6).

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Chapter 3: The role of consciously timed movements in shaping and improving auditory timing

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Abstract

Our subjective sense of time is intertwined with a plethora of perceptual, cognitive and motor functions, and likewise, the brain is equipped to expertly filter, weight and combine these signals for seamless interactions with a dynamic world. Until relatively recently, the literature on time perception has excluded the influence of simultaneous motor activity, yet it has been found that motor circuits in the brain are at the core of most timing functions. Several studies have now identified that concurrent movements exert robust effects on perceptual timing estimates, but critically have not assessed how humans consciously judge the duration of their own movements. This creates a gap in our understanding of the mechanisms driving movement-related effects on sensory timing. We sought to address this gap by administering a sensorimotor timing task in which we explicitly compared the timing of isolated auditory tones and arm movements, or both simultaneously. We contextualized our findings within a Bayesian cue combination framework, in which separate sources of temporal information are weighted by their reliability and integrated into a unitary time estimate that is more precise than either unisensory estimate. Our results revealed differences in accuracy between auditory, movement and combined trials, and (crucially) that combined trials were the most accurately timed. Under

the Bayesian framework, we found that participants' combined estimates were more precise than isolated estimates, yet were sub-optimal when compared with the model's prediction, on average. These findings elucidate previously unknown qualities of conscious motor timing and propose computational mechanisms that can describe how movements combine with perceptual signals to create unified, multimodal experiences of time.

Introduction

Motor control functions are critical to our survival in the world and diverse in nature, spanning multiple time scales and integrating a flood of neural signals to guide us through various tasks [1–3]. Important to movement is the monitoring of sensory information to update movement plans according to errors or environmental demands [4]. In addition, individuals often calibrate ongoing movements to amplify or suppress channels of sensory information according to their goals via 'active sensing' [5], reflecting the continuous and bidirectional nature of the relationship.

It follows that time perception, a high-level, cumulative evaluation of one or more sensory channels, is highly malleable in response to movement characteristics. Although time perception studies have largely excluded concurrent motor components, recent studies focused on arm movements reveal that the accuracy and precision of perceptual timing are affected by a number of movement characteristics such as direction, speed, distance and movement environment [6–10]. Notably, movement can also improve time perception. In a set of complementary experiments, auditory intervals were presented either during arm movements or in the absence of movement. For both temporal categorization and reproduction tasks, intervals encoded during movement were timed more precisely [11]. In a separate temporal discrimination study using auditory intervals, timing precision was enhanced for intervals for which the stimulus onset was determined by the participant rather than passively presented [12]. The benefit of movement is also highlighted in animal behaviour. Rats trained to estimate a

fixed interval to receive a reward learned to use stereotyped movements to enhance the accuracy and precision of their estimates [13].

Given the clear temporal benefit of movement, it is reasonable to ask whether and to what extent it is timed with different levels of accuracy and precision than the sensory channels that much of this work focuses on, and whether these differences can explain how the channels of information are combined. To address these questions, we contextualize our study under a framework of Bayesian cue combination, which posits that multiple channels of timing information are evaluated by their reliability and optimally integrated into a more precise estimate than either alone [14]. Accordingly, the mean of the combined estimates is predicted to gravitate towards the mean of the more precise (i.e. more influential) modality. This framework aligns with principles of multisensory cue combination [15–17], which places importance on signal reliability when combining multiple inputs. Neural data reflect this differential weighting via population responses in multisensory areas [18,19].

This evidence has offered insights upon which to build our understanding of the intersection of motor and timing processes [20]. However, little is known about how self-movements are timed without an added perceptual event. We note that motor control studies certainly include timing components, but the key caveat is that they examine implicit rather than explicit timing. For example, a task might require participants to synchronize their movements to a beat [21] or interact dynamically with a stimulus without probing their conscious evaluation of the passage of time. To the latter point, we refer to conscious awareness of time as explicitly measuring its passage, as distinct from implicit timing mechanisms [22], which may reflect internalizations of cause-and-effect relationships or correlated spatiotemporal measurements [23]. One preliminary study of interest [24] employed a unique paradigm to test explicit timing of durations that were implicitly encoded. Participants were trained on a ‘skittles’ task requiring them to hold and release a virtual ball to hit a target. Repeated practice led them to internalize an optimal duration range for which holding and releasing led to a successful trial. When tested

in an explicit timing task, they exhibited a selective improvement for timing the target interval, while participants who did not play the game showed no benefit. Combined with the previous studies discussed, this supports the hypothesis that movements offer highly reliable temporal measurements that in turn improve timing of concurrent events and even future timing performance. This is further evidenced by increased timing acuity in motor 'experts' such as athletes and drummers [25,26].

Our goal in the current study was twofold: first, we sought to understand how duration of self-movement is evaluated, given that most movement-timing tasks have either focused solely on implicit timing or have not isolated movements from a concurrent perceptual event. Second, we sought to describe differences in motor and auditory timing, and importantly, how these sources of information are combined to form a unitary estimate. We found evidence that there are differences in timing accuracy between motor and auditory estimates, and that durations are both more accurately and precisely timed using both sources of information. Finally, we synthesized these results under a Bayesian cue combination framework to account for the pronounced benefit that resulted from combining motor and perceptual sources.

Methods

Participants

We tested 20 right-handed participants (13 females, 7 males, mean age = 25.45 (9.17)). Handedness was confirmed by the Edinburgh Handedness Inventory [27].

Procedure

Participants performed the experiment using a robotic arm manipulandum (KINARM End-Point Lab, BKIN Technologies [28,29]) that allowed movement along a flat workspace using the right arm. Direct viewing of the robotic arm was occluded by a flat display that allowed viewing of targets and cues via a downward-facing monitor mounted above the workspace. Motor output was sampled at 1000 Hz. Participants were free to adjust the chair so that they could comfortably view the full display.

Trials were divided into encoding and reproduction phases and were structured as follows (figure 1): first, the robotic arm guided participants to 1 of 16 locations in a grid-like array. Then, they experienced one of the three trial conditions. In ‘movement’ trials, subjects began moving until interrupted by an imposed brake (a 100 ms linear increase in resistive force from 0 to 50 N). In ‘auditory’ trials, the robotic arm was locked in the random location and the participant heard an auditory tone. In ‘combined’ trials, subjects were cued to move while timing a concurrent auditory tone; in this condition, the tone began as soon as the apparatus detected movement at the velocity threshold of 5 cm s^{-1} , and the brake was applied synchronously with the auditory tone offset. After the encoding phase, they were guided to a central target for the reproduction phase. When this target turned green, subjects reproduced the encoded duration by holding and releasing a button attached to the handle. The tested durations were 1000, 1500, 2000, 2500, 3000, 3500 and 4000 ms. Trial conditions were experienced in blocks of 14 trials (for a total of 210 trials) in a pseudorandomized order such that no condition was experienced twice in a row.

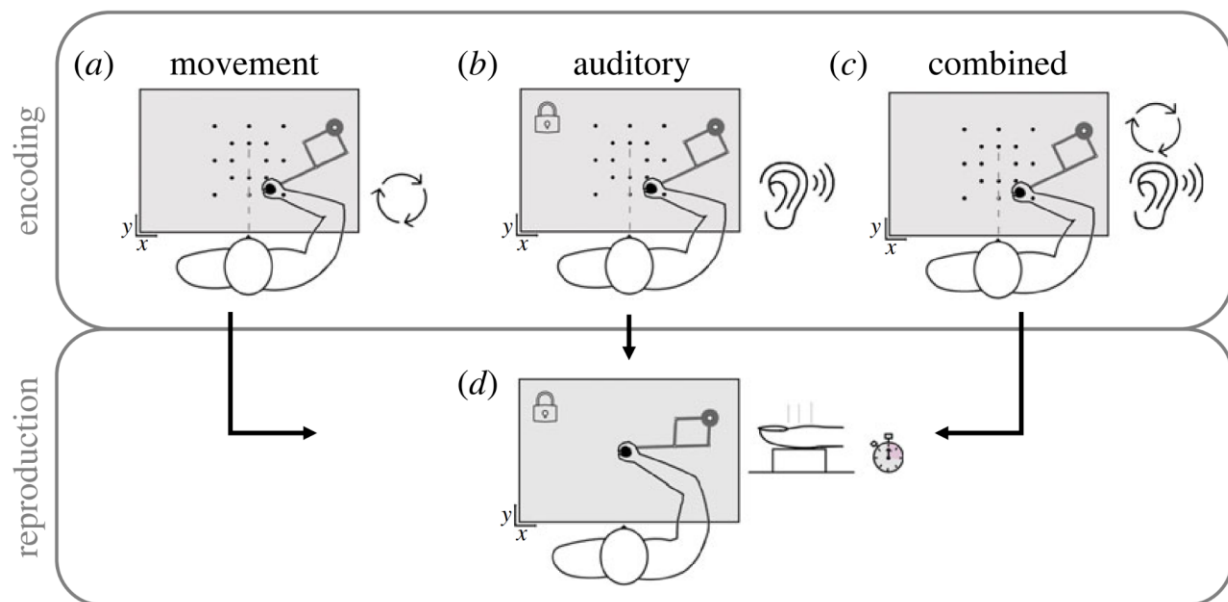


Figure 1. Task schematic. (a) Movement-only trial. The robotic arm guided subjects to a random location (dots not visible during task), and the participant moved freely until interrupted

by a 'brake'. (b) Auditory-only trial. The robot handle was locked in random location, and the participant listened to an auditory tone. (c) Combined movement-auditory trial. The robotic arm was guided to a random location, and the participant moved freely and listened to the auditory tone until the 'brake' was applied along with the tone offset. (d) Reproduction phase. The interval was estimated by holding and releasing a button attached to the handle.

Robotic arm manipulandum data were sampled at 1000 Hz to produce vectors for position, velocity, force and other movement parameters over the course of time for each trial. Trials were excluded if reproduced times fell outside three deviations from the mean (,1% of trials excluded). In addition, trials with movement (movement-only and combined) were excluded if the stop latency after the brake was applied fell outside three scaled absolute deviations from the median (2.9% of trials excluded).

Our first goal was to investigate the relationship between duration and reproduced time to determine timing accuracy. Importantly, movement-only and combined trials were analyzed with respect to time spent moving rather than the pre-specified duration. This is because, in general, participants exhibited a short delay to respond to the movement brake, usually adding up to a few hundred milliseconds on most trials. We directly assessed constant error as a measure of accuracy, defined as the difference between the reproduced duration using the button press and the actual target duration. To measure performance, we applied a linear mixed model (LMM) design, in which response error was the predicted variable, encoded duration and condition were fixed effects, and subject was treated as a random effect.

In addition, we examined the relationships between movement parameters and timing performance. Previous works have shown that arm movements covering a greater distance lead to longer perceived durations [11,30]. Here, we extracted the movement distance for each trial (defined as the Euclidean distance travelled between duration onset and offset) and performed a Spearman partial correlation test between movement distance and reproduced time,

controlling for target duration. Partial correlation values were calculated for each subject separately for movement and combined trial types; each was assessed with a one-sample t-test against a baseline of zero. Multiple comparisons were corrected using the Bonferroni correction.

Statistical analyses were performed using R, JASP ([http:// www.jasp-stats.org](http://www.jasp-stats.org)), and Matlab. For accuracy and coefficient of variation (CV) analyses, we report results from LMMs with subject as a random effect. Results are reported at a significance level of 0.05.

Computational modelling

To determine the sensitivity of each of the unisensory modality conditions, as well as the multisensory combined one, we employed a Bayesian observer–actor model (figure 4) previously described by Remington et al. [31] (see also [32]) and used previously by our group [30]. In this model, sample durations (t_s) are inferred as draws from noisy measurement distributions (t_m) that scale in width according to the length of the presented interval. These measurements, when perceived, may be offset from veridical estimates as a result of perceptual bias or other outside forces (b). Due to the noise in the measurement process, the brain combines the perceived measurement with the prior distribution of presented intervals in a statistically optimal manner to produce a posterior estimate of time (t_e). The mean of the posterior distribution is then, in turn, used to guide the reproduced interval (t_p), corrupted by production noise (p). The resulting fits to this model thus produce an estimate of the measurement noise (m), the production noise (p) and the offset shift in perceived duration (b). Note that the offset term is also similar to that employed for other reproduction tasks as a shift parameter [33]. In addition, the prior used for the model can be either uniform or Gaussian in shape [26], with implications for how these are combined; uniform priors are characterized by the range of intervals presented, whereas Gaussian priors are centred on the average duration presented, with a width dependent on their precision. We chose here to model the prior as a Gaussian, as each individual subject will have experienced a slightly different set of intervals during the estimation phase for each of the three conditions. This is because in the two

movement conditions, the offsets were variable from trial to trial. As such, we modelled the width of individual subject priors to match the width of encoded intervals for each subject (σ_{t_s}). Model fits were conducted by minimizing the negative loglikelihood of subject responses given the sample values using Matlab's *fminsearch* function.

To determine if subjects combined auditory and movement modalities in an optimal manner, consistent with cue combination, we used outputs of the Bayesian model to compare between unisensory and multisensory conditions. Specifically, cue combination predictions that the multisensory combination σ_c of two unisensory estimates (auditory σ_A and movement σ_M) when modelled as Gaussians should equal:

$$\sigma_c = \frac{\sigma_A \sigma_M}{\sigma_A + \sigma_M}.$$

That is, the combined width is the product of the unisensory widths divided by their sum. Since the measurement widths were modelled as Gaussians in our Bayesian model, the unisensory widths from model fits can be used in the aforementioned equation to produce an estimate of the predicted width. Further, as the model also provides a width for the multisensory, combined condition, we can compare the width observed with that predicted by cue combination [17,34]. If the predicted and observed widths are not statistically different, then subjects combined unisensory estimates optimally, whereas larger observed widths than predicted indicate sub-optimal combination [35].

Results

The temporal reproduction group data are illustrated in figure 2. As described earlier, movement-only and combined trials were analyzed with respect to time spent moving, which we defined as the predetermined interval (1000, 1500, 2000, 2500, 3000, 3500 and 4000 ms) plus the 'stop latency' (figure 2d), defined as the time it took participants to stop movement after the brake was applied. We used a linear mixed effects model with trial type (movement and combined levels only) and duration as fixed effects and subject as a random effect to test for

stop latency differences related to trial type or duration. There were no significant main effects of trial type [$F(1, 2650.03) = 0.056, p = 0.812$] or duration [$F(1, 2650.36) = 0.014, p = 0.906$], and no significant interaction [$F(1, 2650.01) = 1.622, p = 0.203$]. In the rest of the figures, the target durations for movement and combined trials include these stop latencies, which are shown with horizontal error bars to denote the standard error (figure 2a–c).

We next employed a linear mixed effects model with trial type and duration as fixed effects and subject as a random effect to characterize how these variables affected reproduced duration. We did this analysis using constant error values (reproduced duration – target duration) rather than raw reproduction values as the dependent variable, as they represent the same underlying data but provide information about the direction and magnitude of errors (figure 2b). Model terms were nested using the Satterthwaite method. The model revealed a significant interaction of duration and trial type [$F(2, 4045.04) = 30.577, p < 0.001$], and main effects of trial type [$F(2, 4045.05) = 5.512, p = 0.004$] and duration [$F(1, 4045.15) = 821.134, p < 0.001$]. We examined the estimated marginal means and contrasts of trial types with Holm-adjusted p-values, which revealed a significant difference between auditory (EMM = 180.185, CI[- 25.003, 385.374]) and movement (EMM = -51.534, CI[- 256.860, 153.791]) trials (contrast = 231.720, SE = 20.915, $p < 0.001$), combined (EMM = 81.551, CI[- 123.649, 286.751]) and auditory trials (contrast = -98.635, SE = 20.592, $p < 0.001$), and finally, between combined and movement trials (contrast = 133.085, SE = 20.940, $p < 0.001$). We also compared the estimated marginal means to zero and did not find a significant result for any of the trial types ($p_{\text{auditory}} = 0.085, p_{\text{movement}} = 0.623, p_{\text{combined}} = 0.436$).

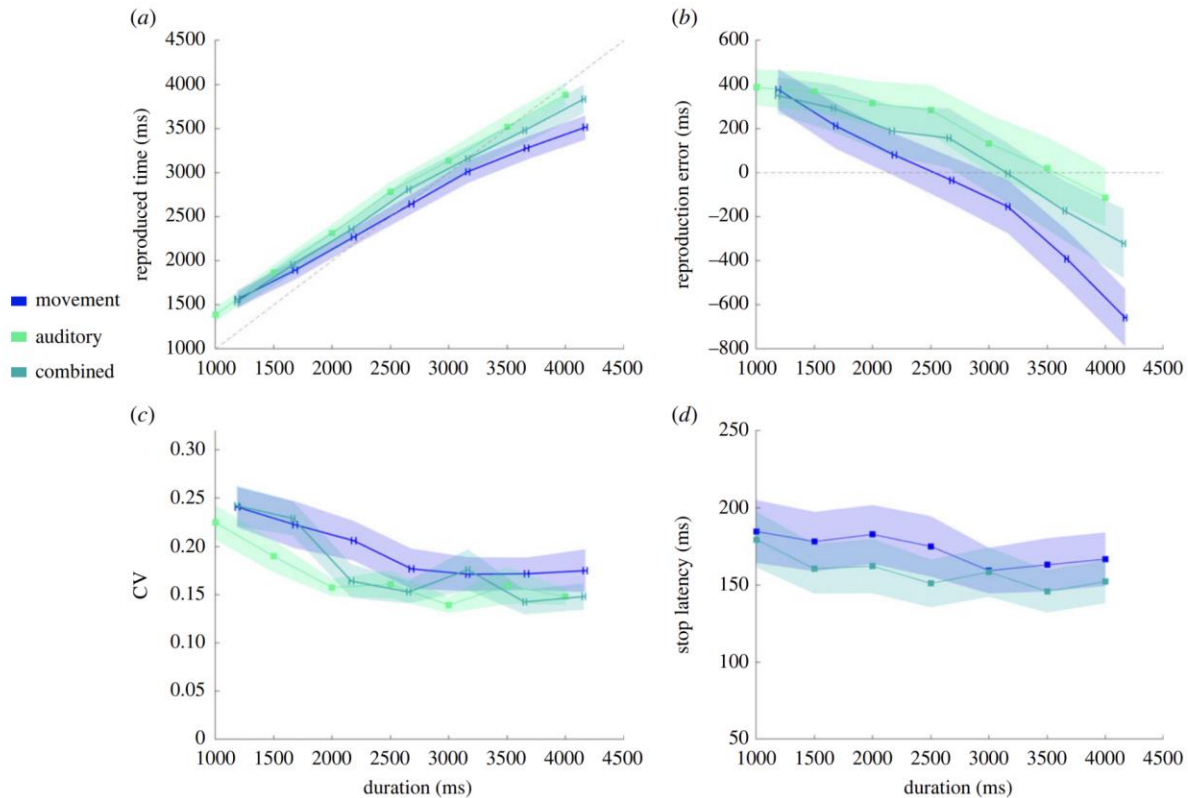


Figure 2. Temporal reproduction results. (a) Reproduction performance plotted as a function of target duration and trial type. Shaded vertical error bars represent reproduction standard error, and horizontal bars represent standard error of time spent moving for movement and combined trials. (b) Constant error values (reproduced duration – target duration) as a function of target duration and trial type. (c) Coefficient of variation (std/mean) of reproduction time as a function of target duration and trial type. (d) Stop latencies of movement and combined trials when the movement brake was applied. These values plus the fixed target durations (x-axis) determined target durations for trials with movement.

Our next analysis focused on the error slopes produced by the different trial types. This analysis reveals the degree of central tendency (i.e. attraction of estimates towards the mean). A significant slope difference was found between all trial types pairs (auditory – movement = 0.161, SE = 0.021, $p < 0.001$; combined – auditory = -0.061, SE = 0.021, $p = 0.003$; combined

– movement = 0.101, SE = 0.021, $p < 0.001$). Movement trials exhibited the lowest slope, and auditory trials exhibited the highest slope.

Next, we examined the CV as a measure of reproduction precision across durations and trial types. We employed a LMM with trial type and duration as fixed effects and subject as a random effect and found that the CV varied as a function of duration [$F(1, 395.18) = 64.227$, $p < 0.001$] but not the trial type [$F(2, 395.05) = 2.575$, $p = 0.077$]. The interaction of the trial type and duration was not significant [$F(2, 395.05) = 0.893$, $p = 0.410$].

We were additionally interested in the relationship between movement parameters and reproduced time, particularly for the combined trial type. We assessed this effect by performing subject-level partial correlations between Euclidean movement distance during duration encoding and the subsequent reproduced duration, controlling for target duration. The distribution of individual correlation coefficients is displayed in figure 3. By using a one-sample t -test, we found that the values were distributed significantly above zero for both motor [$t(19) = 2.974$, $p = 0.008$, Cohen's $D = 0.665$] and combined [$t(19) = 4.278$, $p < 0.001$, $D = 0.957$] conditions, indicating a positive relationship between movement distance and reproduced duration, and replicating prior work that movement distances are associated with longer estimated durations [11,30].

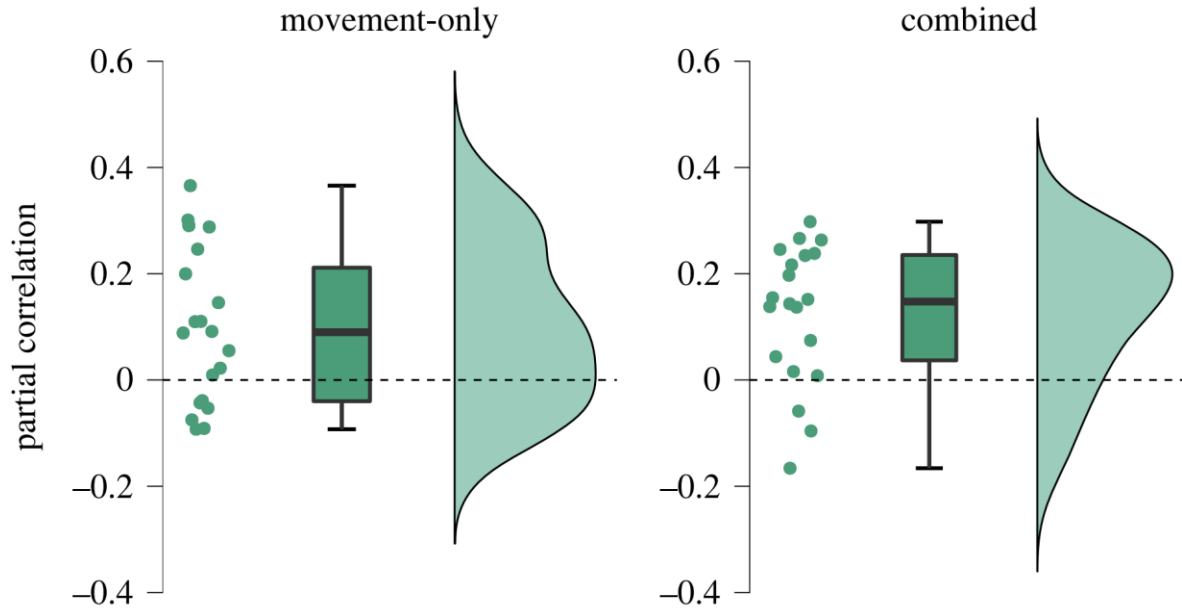


Figure 3. Effects of movement on duration estimates. Spearman partial correlation coefficients are displayed for each subject as raincloud plots in both the unisensory, movement-only condition and the multisensory, combined condition. For each subject, partial correlations were calculated as the association between single-trial reproduced durations and the movement length during the encoding phase, while controlling for duration. On average, the correlation coefficients in both groups were significantly greater than zero.

Cue Combination

To examine the impact of modality on time estimates, we further fit reproduced durations with a Bayesian observer–actor model. The results of our model fits provided estimates of the measurement noise (m), production noise (p), and offset (b) for each modality. Repeated-measure analyses of variance for each parameter revealed only a main effect of condition for measurement noise [$F(2, 38) = 2.133, p = 0.039$], with all other parameters being non-significant (all $p < 0.05$). For the noise parameter, measurement noise scores were significantly lower for the combined condition compared to movement [$t(19) = -2.118, p = 0.048$], but not auditory intervals [$t(19) = -1.682, p = 0.109$] (figure 4). Due to our a priori hypothesis that the combined

multisensory estimates would be better than both unisensory estimates, we averaged auditory and movement measurement widths and compared them to the combined measurement noise, where a significant difference was observed [$t(19) = -2.15$, $p = 0.045$].

To compare with the predictions of the cue combination model, we used the unisensory measurement noise widths to generate a predicted width for their optimal combination. That is, the product of the unisensory widths divided by their sum. Here, we observed that the predicted widths were on average lower than the observed widths from the combined multisensory condition [$t(19) = 6.111$, $p < 0.001$] (figure 4). In addition, we observed a strong correlation between observed and predicted widths [$r(18) = 0.654$, $p = 0.002$], indicating that the cue combination equation provided a good prediction of multisensory noise, even if the observed estimates were sub-optimal. As a further observation, we noted that subjects with lower multisensory noise estimates were closer to the optimal prediction, a finding we confirmed quantitatively through the correlation of multisensory widths with the difference between those widths and the predicted estimate [$r(18) = -0.883$, $p < 0.001$]. As a final check, we compared subjects who exhibited smaller unisensory widths for one modality (e.g. auditory) over the other (e.g. movement). No differences were observed between subjects with greater precision in either modality, for either the multisensory combined estimates [$t(18) = 0.765$, $p = 0.454$] or the difference from optimality [$t(18) = -0.528$, $p = 0.604$], indicating that improved estimates for neither unisensory modality conveyed a special benefit in cue combination.

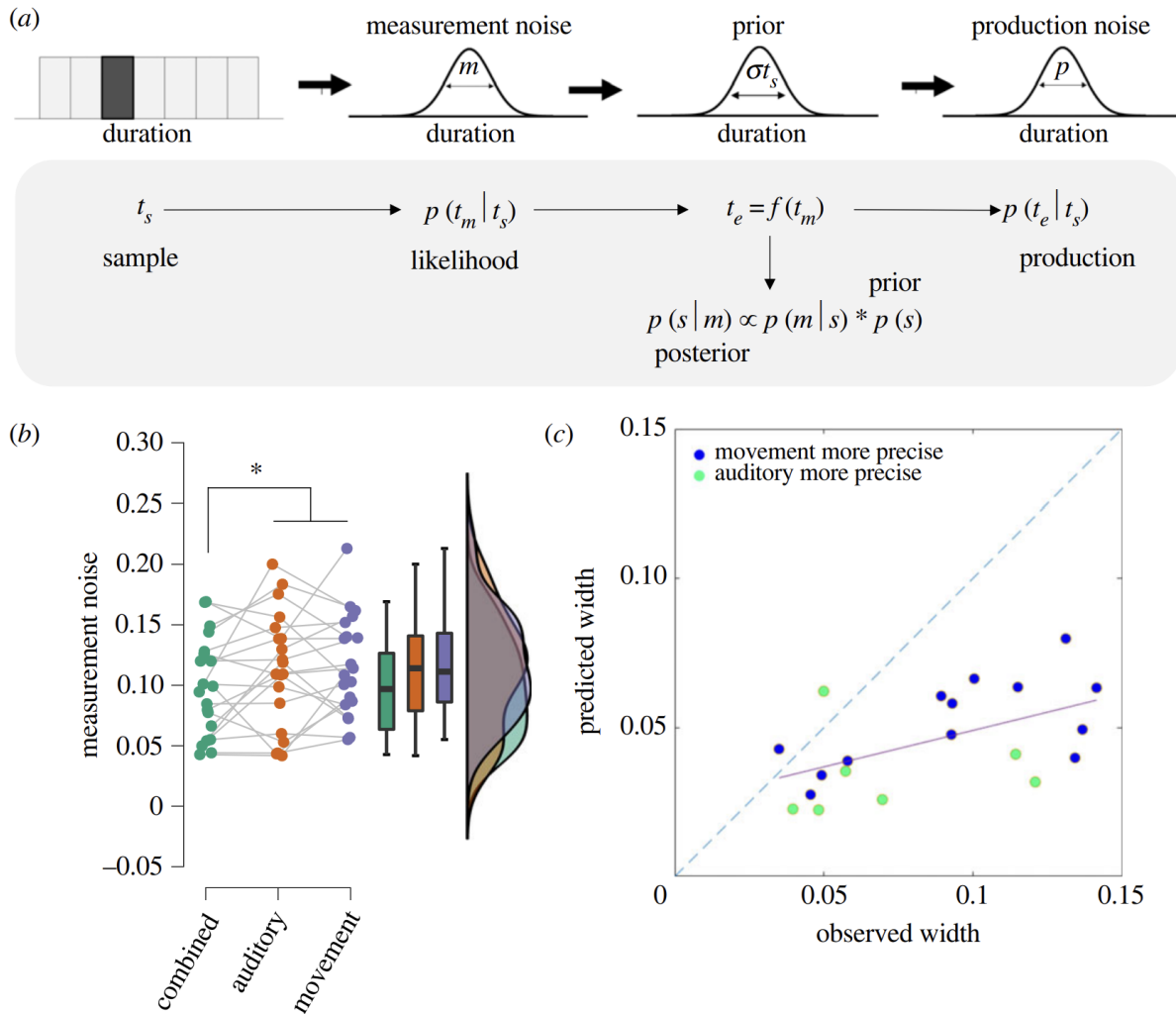


Figure 4. Bayesian observer–actor model for time estimates. (a) Schematic of the model, in which a sample interval presented on a given trial t_s is perceived with some measurement noise from a Gaussian distribution with width m . This estimate is then combined with a prior distribution of previously experienced intervals, also characterized as a Gaussian, with width σt_s to form a posterior estimate t_e . During reproduction, the posterior estimate is further corrupted by motor production noise as a Gaussian distribution with width p . For model σt_s , m and p were set as free parameters, whereas σt_s was measured directly from the experienced sample intervals for each subject. (b) Model fits for the measurement noise width (m) for all three modality conditions. We observed that the multisensory, combined measurement noise was significantly lower than both the unisensory auditory and movement conditions, together. (c)

Scatterplot comparing the observed multisensory width to the predicted width given by combining both of the unisensory widths together via cue combination. Here, we observed that the observed widths fell on average below the predicted width, yet were also significantly correlated. Individual points are coloured based on which of the unisensory widths was smaller (more precise); no differences were found between either of these groups.

Discussion

We administered a temporal reproduction experiment in which we tested timing performance for auditory and motor timing, and both simultaneously. Measuring these two sources of information allowed us to assess how self-movements are judged in comparison to auditory tones and shed light on the computational mechanisms that drive movement-related improvements previously observed during perceptual timing tasks [9,11]. We found that modality significantly impacted reproduction performance, such that motor trials resulted in shorter estimates than auditory trials. Critically, combined trials were estimated most accurately, suggesting that the natural biases introduced by auditory and motor intervals oppose each other, but ‘work together’ to form the most veridical estimate based on the information available. In addition, our results fit into a framework of Bayesian cue combination in which multimodal interval measurements are more precise than unisensory measurements [14]. We also found that the reproduction slope was lowest for the movement condition, indicating a greater degree of central tendency compared to the other conditions. An unanswered question is the extent to which this reflects intrinsic properties of movement interval timing, such as a greater reliance on an internalized prior distribution [26] or a general susceptibility towards underestimation as target durations increase.

These results corroborate previous accounts of movement enhancing cross-modal timing [11–13,36,37]. However, it is of interest whether this is accomplished in an optimal fashion. According to the Bayesian cue combination framework, we predicted that the

measurement noise (i.e. distribution width) of the combined condition would be lower than for unimodal conditions. The model results indicated that the measurement noise of the combined condition was significantly lower than for movement and auditory conditions together. While we did not observe meaningful differences in coefficient of variation (an index of variability that is often tied to precision [38,39]) between trial types, we suggest that the measurement noise parameter is a more useful indicator of precision in our experiment given that the target durations were not fixed for trials that involved movement, and further that this measure attempts to remove motor production noise. We next compared the observed measurement noise to the model prediction that would indicate optimally combined estimates. The observed and predicted values were significantly positively correlated, although we note that participants generally combined sub-optimally. This pattern was not dependent on which unimodal condition was more precise for individual participants. The model also predicts that during optimal multimodal timing, the mean reproduction estimate should gravitate towards the more precise modality; however, given that we did not find overall differences in unimodal timing precision across participants and performance was generally sub-optimal, this prediction was challenging to test in the current paradigm. However, we note that sub-optimality in human perception is a commonly observed feature, which may depend on multiple other factors beyond movement [35]. Remarkably, this lack of difference highlights that movement timing is at least as precise as auditory timing, which until now has been documented as the most precisely timed modality [40–42]. Future work may assess this prediction more closely where larger differences between unimodal conditions exist (e.g. visual timing).

We have described some computational principles by which motor and sensory information may be combined for a more precise multimodal estimate. These perspectives are strengthened by discussing their relation to neural mechanisms. There is a great degree of functional overlap between motor and timing activity in brain regions considered vital to motor control, with greater representation of supra-second intervals in cortical regions and sub-second

intervals in subcortical regions like the cerebellum [43,44]. The supplementary motor area (SMA) stands out as a region of interest, as it is activated across a wide range of timing tasks and encodes time intervals in neurons organized along a rostrocaudal ‘chronotopic’ gradient [45]. In addition, the SMA exists within a larger cortico-thalamic-basal ganglia timing circuit [20] that encodes intervals, integrates multiple sensory inputs [46], and sends predictive signals to sensory areas.

By using these insights, we have outlined two possibilities to describe the neural implementation of movement-related timing effects [14]. The first possibility, feedforward enhancement, posits that these effects are instantiated in motor circuits and sharpen duration measurements via corollary feedback to motor regions like the SMA, thereby sharpening the tuning of duration-selective neurons. The SMA is equipped to respond to these signals via white matter connections with the primary motor cortex, basal ganglia and spinal cord [47], all of which require a high degree of temporal coordination during movement control. In addition, deep reinforcement learning agents with feedforward modules (and no recurrence) successfully learn to produce temporal intervals by generating stereotyped trajectories in their environments [48].

The second possibility, active sensing [5], proposes that motor activity acts on earlier sensory regions to enhance cross-modal temporal measurements. Outside of the timing domain, this is a well-established process. For example, auditory perception is enhanced when a sound is triggered by an action [49], and accordingly, motor preparation has been found to elicit responses in the auditory cortex [50]. There are also several examples tying motor activity to changes in visual processing [51–55]. The active sensing hypothesis is compatible with prior research on multisensory integration, as it essentially describes the convergence of multiple signals to shape neural computations. A classic example is the superior colliculus, which integrates visual, auditory, and sensorimotor signals (among others) to guide eye and head movements [56,57]. These signals are not localized to dedicated hubs, but rather occur

throughout the neocortex [58], and have been proposed to reflect generalizable ‘canonical operations’ (e.g. divisive normalization and oscillatory phase resets) when integrating a diverse range of inputs—including from motor circuits [59]. For example, saccade onsets elicit time-locked local field potential changes in primary visual cortex [60]. The active sensing hypothesis has empirical support from several lines of research and can build upon known neural integration mechanisms—more generalizable than previously thought—to shed light on how movement can improve timing.

We have primarily discussed our results with a focus on the ability of motor activity to shape auditory timing. However, it can also be said that the enhancement is bidirectional (i.e. movement timing improves with added auditory information). In a related fashion, one study found that auditory intervals trained in a temporal discrimination task selectively improved timing precision for the same intervals in a subsequent motor task [61]. These behavioural effects are paralleled by brain circuitry, particularly in the dorsal auditory stream with bidirectional connections between hubs in the auditory cortex, inferior parietal lobule, and premotor cortex [62]. This pathway has been highlighted as essential to speech and music perception and production, especially for auditory predictive processes [62–64]. Further, the dorsal auditory pathway uses predictive mechanisms to support beat perception as described in the action simulation for auditory prediction (ASAP) hypothesis [65,66]. Although our study’s focus was on interval timing rather than beat timing, the dorsal pathway’s important role in auditory perception may have implications for our observed results [67].

Beyond basic neuroscience, this work has implications in clinical disorders associated with motor and timing deficits such as Parkinson’s disease and Huntington’s disease [68–71]. These parallel deficits are not restricted to movement disorders, but occur in psychiatric or neurodevelopmental conditions such as schizophrenia and attention deficit hyperactivity disorder [72,73]. Motor training has shown some usefulness in rehabilitation and symptom management; Parkinson’s patients have been found to reduce their gait variability when

exposed to rhythmic auditory stimuli that can adaptively synchronize with their steps [74]. Critically, this improvement may depend on the optimality with which patients incorporate these two sources of temporal information, and so by adopting a baseline measurement, one could track improvement over time. In stroke patients, fine motor skills are re-learned more effectively with musical motor training than functional motor training [75]. Thus, many benefits of movement training rely strongly on integrating relevant sensory information, and based on this evidence, interactions between motor and auditory interval timing may be a promising avenue to explore in the treatment and diagnosis of movement disorders.

In conclusion, while converging evidence suggests a powerful role of movement in shaping time perception [14,76], studies have focused primarily on perceptual timing with movement as an added component without isolating how movements are consciously timed on their own (i.e. how movements are incorporated when subjects are explicitly engaged in estimating time [22]). Our experiment provided the distinct advantage of isolating and comparing timing in movement and auditory modalities, in addition to testing predictions about their integration under a Bayesian cue combination framework. We found that multisensory timing was superior to unisensory timing as reflected in the higher accuracy of combined estimates, and in addition, measurement noise of combined estimates reflected at least some degree of optimal cue combination (with the caveat that participants often perform sub-optimally compared to computational models). This study thus addresses a prior gap in knowledge where consciously timed self-movement were not well understood, especially in relation to timing in other modalities. We also expanded on a growing body of research on movement-timing effects, first by describing potential computational mechanisms that drive them, and ways they may be instantiated in neural circuits.

Ethics. Procedures were approved by the University of California, Davis Institutional Review Board.

Data accessibility. We have uploaded our data to Dryad, which can be accessed at <https://doi.org/10.25338/B8FD0N> [77].

Authors' contributions. R.D.: conceptualization, data curation, formal analysis, methodology, validation, visualization and writing—original draft; W.Z.: data curation, formal analysis, methodology and software; P.D.: methodology; W.M.J.: conceptualization, funding acquisition, methodology, resources, software, supervision and writing—review and editing; M.W.: conceptualization, formal analysis, funding acquisition, supervision, validation, visualization and writing—review and editing. All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. We declare we have no competing interests.

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Chapter 4: Assessing the impact of movement on time perception in adults with ADHD

Abstract

Adults with attention deficit hyperactivity disorder (ADHD) exhibit differences in time perception compared to the general population. While existing results are heterogeneous regarding timing precision and accuracy, the differences (and in many cases, deficits) are a point of interest in understanding adult ADHD and making improvements to patients' quality of life. In recent years, the study of time perception has shifted towards uncovering the vital role of the motor system in perceiving the passage of time. Neural data show that motor regions in the brain are consistently activated by timing tasks, and motor manipulations in behavioral tasks lead to changes in timing performance. In the current study, we tested whether movement would enhance timing precision in adults with ADHD compared to a control group. Participants made temporal judgments about auditory tones while manipulating a robotic handle in the "movement" condition or being locked in place in the "hold" condition. Trial types were presented in a block design. Our results show that compared to controls, the ADHD group estimated time intervals as shorter, with no significant differences in precision. Surprisingly, we found no significant effect of movement condition on either accuracy or precision. We contrast our findings with prior studies and suggest that more research is needed to better understand the heterogeneity of timing in adults with ADHD.

Introduction

Attention deficit hyperactivity disorder (ADHD) is a neurodevelopmental disorder that begins in childhood and frequently persists into adulthood. Some of the most prominent symptoms of ADHD are inattention, hyperactivity, and impulsivity. These symptom clusters are also used to define clinical subtypes, primarily inattentive, primarily hyperactive/impulsive, and combined. One symptom of ADHD that can cause challenges to daily functioning is a deficit in time perception and time management. For example, people with ADHD commonly report

difficulties being on time to work or keeping appointments. While children with ADHD may be able to avoid some of the negative consequences of poor time management by having parental assistance, adults with ADHD can face more severe consequences such as losing their source of employment. Despite the importance of understanding how adults with ADHD perceive time, studies on this topic are uncommon in the existing literature (Mette, 2023). One of our goals in conducting this study was to elucidate how adults with ADHD perceive time on the scale of seconds.

The study of time perception can take many approaches, such as testing different time scales, paradigms, and sensory modalities. Additionally, studies in recent years have taken a novel approach to understanding time perception through the lens of movement (De Kock et al. 2021a). Timing can certainly be conceptualized as a perceptual process, but perceptual experiences are rarely passive and usually involve interactions with our environment. Principles such as active sensing and efference copy illustrate this idea; we often coordinate our movements to amplify or suppress sensory signals, and our brains utilize feedback connections between motor and sensory systems to predict the sensory consequences of our actions to optimize future movement strategies. Further, ADHD is associated with notable differences in motor characteristics, such as spatial and temporal variability of movement execution (Mostofsky et al. 2006), immature and impulsive responding (Dahan & Reiner, 2017; Mulder et al. 2010), task-irrelevant motor output (Mihali et al. 2018) and structural and functional brain differences in motor regions (Castellanos et al. 2002, Fassbender et al. 2011, Mostofsky et al. 2006). This intersection of motor and timing processes presents an interesting avenue to study time perception in ADHD. Several findings have emerged linking the motor system to the timing of intervals. The most striking evidence is shown in neuroimaging data, where across 84 studies, timing tasks consistently activated motor regions in the brain (Nani et al. 2019). This is further supported by behavioral data, where studies that involve movement in timing tasks reveal strong influences of movement on timing performance. For example, temporal intervals

are perceived as shorter when accompanied by short arm movements as opposed to long arm movements (Yon et al. 2017; De Kock et al. 2021b). One particular study from our prior work indicated that individuals who were allowed to move during a timing task experienced a significant advantage to timing precision compared to individuals who were not allowed to move (Wiener et al. 2019). More generally, movement may offer other benefits to individuals with ADHD; for example, children with ADHD have been shown to improve their cognitive control performance during trials accompanied by fidgeting (Hartanto et al. 2016).

Bringing these bodies of knowledge together, our goal for this study was to evaluate the role (and potential benefit) of movement during a time perception task, comparing adults with ADHD to typically developing controls. Participants were tested on a temporal discrimination task in which they were instructed to move in some trials and prevented from doing so in others. We hypothesized that the timing precision would overall be lower in the ADHD group than in the control group, and that timing accuracy would not differ between groups (Mostert et al. 2015). We also hypothesized that movement would improve timing precision as seen in our prior work (Wiener et al. 2019), and that this effect would be more pronounced in the ADHD group. Finally, we hypothesized that accuracy would not be affected by movement condition.

Methods

Recruitment and screening

We recruited participants from the UC Davis campus and surrounding community using fliers, social media posts, and a participant database from a previous ADHD study at the UC Davis MIND Institute. All potential participants were pre-screened via Zoom or phone call. The eligibility criteria and the methods to confirm them are shown in Table 1. In special cases, we made exceptions to particular criteria that we have noted in the table with our justification. In addition to the screening questionnaires, we collected demographic information to report to our funding source. Screening questionnaires were evaluated by a clinician to determine if eligibility requirements were met. All protocols in this study were approved by UC Davis' Institutional

Review Board and participants were paid \$15/hour in gift card credit for their time spent on the screenings and experiment.

Inclusion and Exclusion Criteria	Screening Method
Must be between 18-50 years old	Pre-screen (self-report)
Cannot be blind, color blind, or have corrected vision worse than 20/30 <ul style="list-style-type: none"> - We made one exception for a participant who was colorblind because the task focused on auditory judgments and did not include colored stimuli that would affect their ability to complete the task 	Pre-screen (self-report)
Cannot have any eye disease or any disease that affects the brain	Pre-screen (self-report)
Cannot have had eye or eye muscle surgery, or a history of eye patching for a lazy eye <ul style="list-style-type: none"> - We made one exception for a participant who had undergone lazy eye surgery because they did not have visual or eye movement impairments that would affect their ability to do the task 	Pre-screen (self-report)
Cannot have limited range of arm movement due to disease or injury	Pre-screen (self-report)
Must be able to sit up for the required period	Pre-screen (self-report)
Cannot have a hearing impairment or other disorder that may interfere with task performance	Pre-screen (self-report)
Must be able to read and write	Pre-screen (self-report)
Cannot have currently prescribed psychoactive medication that might affect motor performance (with the exception of stimulant medication for participants with ADHD)	Pre-screen (self-report)
Cannot have significant depression or a psychotic disorder	DSM-5 Mini-International Neuropsychiatric Interview (MINI). ADHD participants were interviewed by a clinician or clinical trainee, and control participants completed a self-

	report questionnaire sent via email.
Cannot have Autism	Autism Spectrum Quotient (ASQ) questionnaire
Participants in the ADHD group must be confirmed to have ADHD	DSM-5 MINI Barkley Adult ADHD Rating Scale—IV (BAARS-IV) <ul style="list-style-type: none"> - Self-Report - Current Symptoms - Other-Report - Childhood Symptoms (completed by an observer who was close to the participant during childhood) - Other-Report - Current Symptoms (completed by an observer who regularly interacted with the participant)
Participants in the control group must be confirmed to not have ADHD by the study team	Same as above, but controls were expected to not endorse ADHD in any questionnaires
Cannot have IQ less than 85	Wechsler Abbreviated Scale of Intelligence 2 (WASI-II) or NIH Toolbox - Picture Vocabulary Test

Table 1. Inclusion and exclusion criteria. Criteria are shown in the left column and methods of confirmation are shown in the right column.

Our final participant pool included 20 controls (mean age = 20.4) and 17 ADHD participants (mean age = 25.31). The gender breakdown included 19 women and 1 man in the control group, and 8 women, 4 men, and 4 non-binary or gender nonconforming individuals in the ADHD group.

Experiment

Participants were given an auditory temporal categorization task during which they listened to 440 Hz tones ranging in duration from 1000-4000 ms (1000, 1260, 1580, 2000, 2520, 3170, and 4000 ms) and decided if they were “short” or “long” based on all tones heard so far (reference-free categorization). The task was performed using a robotic arm manipulandum (KINARM End-Point Lab, BKIN Technologies; Nguyen et al., 2019; Hosseini et al., 2017). This

apparatus allowed participants to manipulate a cursor on a screen using a robotic arm that could move along a two-dimensional plane. Cursor coordinates and other movement parameters were recorded at 1000 Hz.

Participants moved the cursor to a centralized target to begin each trial. The trial structure and conditions are shown in Figure 1. In the “hold” condition, the robotic arm was locked in a central location during the auditory tone, then was released in order for the participant to make their choice while the words “Get ready: Hold” appeared on the screen. In the “movement” condition, the hold on the robotic arm was released after 1000 ms, and the words ‘Get Ready: Move’ appeared on the screen. At this time, the participant could move freely during the tone then make their choice when it elapsed; if a response was made prematurely, the trial would be discarded and repeated. Choices were made by reaching to a “short” (left) or “long” (right) target, placed at 105° and 75° relative to the start location. Although this consistent mapping might be thought of as a confound that could affect choice behavior via motor or spatial biases, we verified in a previous study that the mapping had no significant effect on behavior by assigning half of our participants to a “short” = right and “long” = left mapping (De Kock et al. 2021b). Before testing, participants completed a short practice block for each condition to familiarize themselves with the task. There were 280 total test trials, and movement conditions were experienced in ten blocks of 28 trials each. The block order was pseudorandomized such that no condition was experienced for more than two blocks in a row.

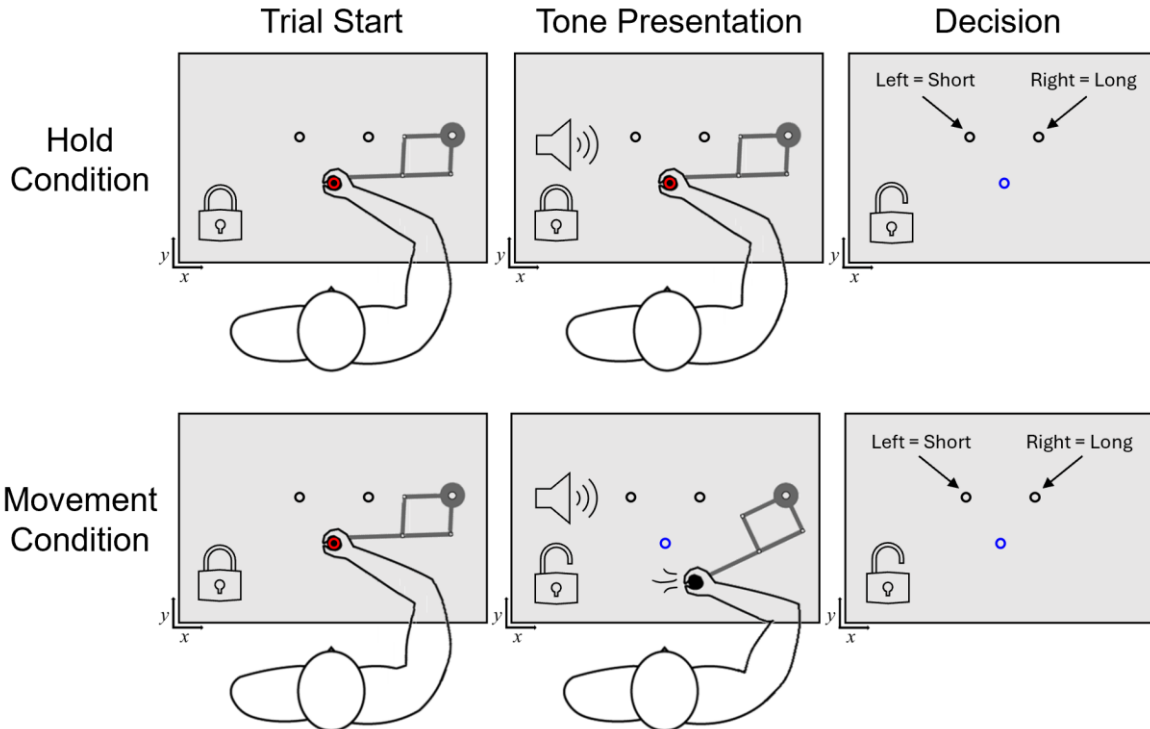


Figure 1. Experiment Schematic. Participants begin each trial in a central location, where the handle is initially locked in place. During the tone presentation, the handle is either locked in place (hold condition) or it is unlocked, allowing free movement (movement condition). During the final decision stage, they categorize the duration as “short” or “long” by moving the cursor into the selected target.

Analysis

From each trial, we collected data about choice (“short” or “long”), response time (RT; time from tone offset to reaching the choice target), and movement distance (summed point-by-point Euclidean distance for each millisecond during the tone presentation). Trials were considered outliers and excluded if RT values were greater than three standard deviations away from a participant’s mean of their log-transformed RT distribution (Ratcliff, 1993). Using the choice data for each participant, we plotted the tone duration against the proportion of “long” responses (P_{long}) to produce a psychometric function fitted with a cumulative Gumbel distribution (this distribution is appropriate due to the intervals being log-spaced; Wiener et al., 2018;

Wiener et al., 2019). One parameter of interest extracted from this distribution that indicates accuracy or bias is the bisection point (BP), the duration at which participants are equally likely to respond “short” or “long”, and for which higher values indicate interval underestimation and lower values indicate interval overestimation. The second parameter is the coefficient of variation (CV), calculated as half of the difference between the intersecting durations at 0.75 and 0.25 P_{long} divided by the BP, and is an index of precision for which lower values indicate higher precision and vice versa. We used the psignifit 4.0 software package in Matlab to estimate individual BPs and CVs (Schütt et al., 2016). For statistical analyses, we employed repeated measures ANOVAs to analyze BPs and CVs as a function of group and movement condition. We also used linear mixed models with subject as a random effects variable to analyze reaction times as a function of group and movement condition, and movement distance as a function of group and duration (movement trials only).

Results

Our analysis of BPs found a significant effect of group [$F(1,35)=9.607$, $p<0.01$, $\eta^2 = 0.203$], but no significant effect of movement condition ($p>0.05$) or a group x movement condition interaction ($p>0.05$; Figure 2a). Bonferroni-corrected post-hoc tests revealed that BPs were higher in the ADHD group ($p<0.01$), indicating that intervals were perceived as shorter (i.e., time perception slowed down). Our analysis of CVs found no significant effect of group, movement condition, or a significant group x movement interaction ($p>0.05$; Figure 2b).

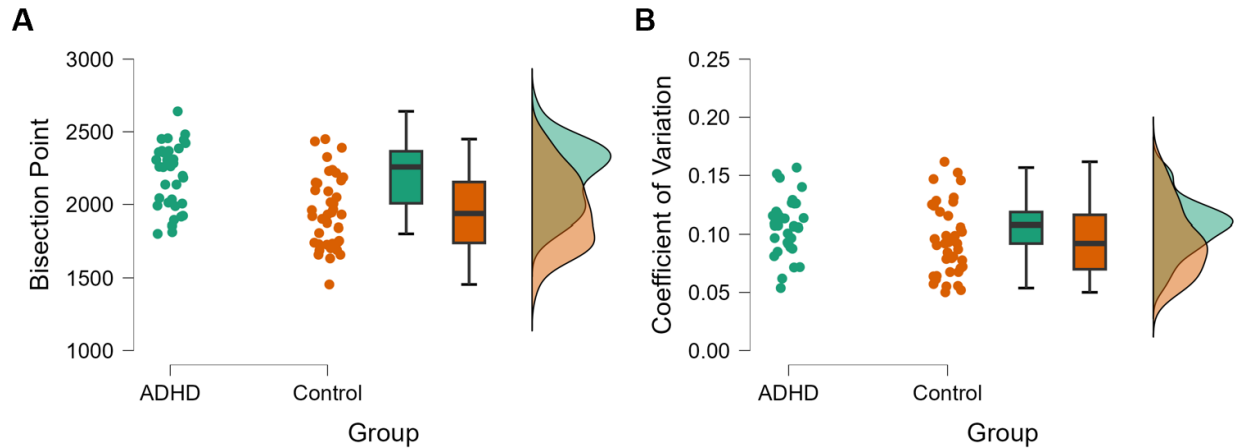


Figure 2. Bias and accuracy comparisons between groups. **(A)** Bisection points (BPs) plotted by group. **(B)** Coefficient of variation (CV) values plotted by group. Distributions of participant values are shown on the right of each plot.

Next, we examined the effect of group and movement condition on RT (Figure 2). First, we found a significant effect of duration [$F(6,49.65)=24.941, p<0.001, \eta^2=0.75$]. These data followed a common pattern observed in temporal categorization tasks similar to an inverted “U”, for which the extremes of the duration range (especially the longest durations) are more quickly judged while the more ambiguous intermediate durations take longer to judge. We also found a significant group x duration interaction [$F(6, 49.65)=2.146, p<0.05, \eta^2=0.226$], for which the participants with ADHD and controls displayed a similar RT pattern as a function of duration, but the peak of the function was less defined for those with ADHD, showing similar RT values for the durations of 2000 and 2520 ms. The RT for the duration of 2520 ms was higher in the ADHD group ($p<0.05$). This parallels our finding that the ADHD group’s bisection point was shifted forward compared to controls; since the most ambiguous duration occurred later, it follows that the RT would also remain elevated at a later point in time. Additionally, we observed a significant movement condition x duration interaction [$F(6,55.20)=3.251, p<0.01, \eta^2=.261$]. Post hoc contrasts specified that RTs were shorter in the movement condition for durations 3170 ($p<0.05$) and 4000 ms ($p<0.01$). This was likely due to the ability to approach the “long” target

as these durations unfolded and make the response from a shorter distance (and therefore, more quickly) than in the hold condition. There was no significant effect of group on RT ($p>0.05$).

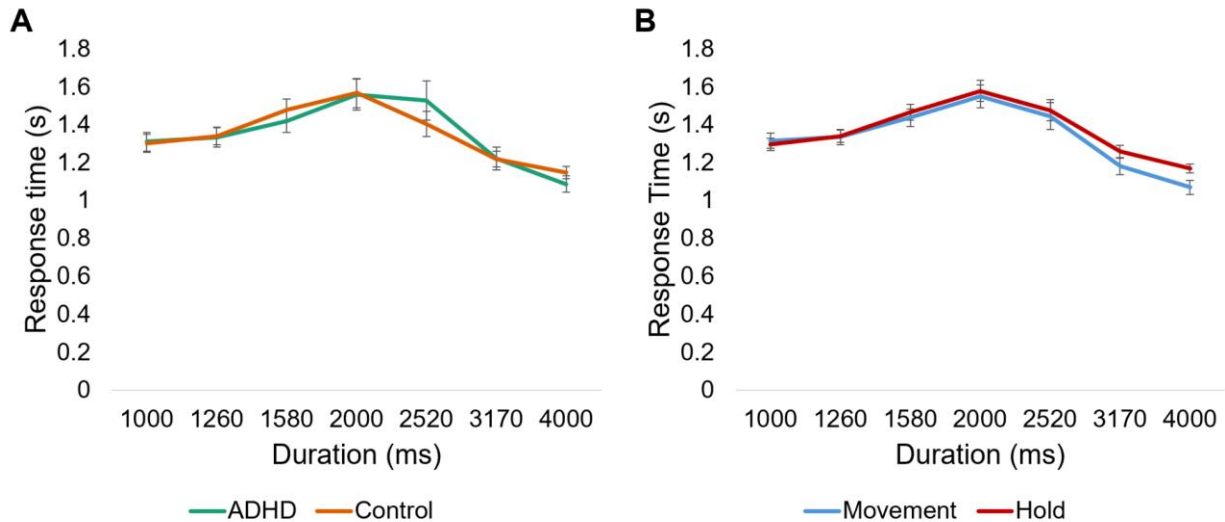


Figure 3. Response time (RT) results. **(A)** RT plotted as a function of group and duration. **(B)** RT plotted as a function of movement condition and duration.

We also analyzed movement distance as a function of group and movement condition (Figure 4). This yielded a significant main effect of duration [$F(6,88.65)=5.085$, $p<0.001$, $\eta^2=0.225$]. As expected, movement distance increased as duration increased. However, there was no significant effect of group or a group x movement condition interaction ($p>0.05$).

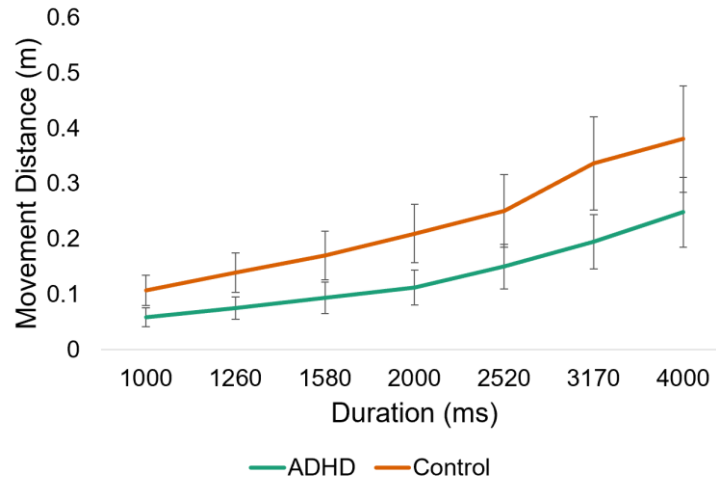


Figure 4. Movement distance results (movement trials only) plotted by duration and group.

Discussion

In this study, we tested the effect of movement on time perception in adults with and without ADHD. Based on prior findings that movement improves timing precision in a general, non-clinical sample of participants, we tested whether these results would generalize to people with ADHD. Our original hypothesis stated that all participants would experience a movement-related improvement to timing precision, and this would be more pronounced in the ADHD group. Instead, several unexpected yet interesting findings arose.

First, people with ADHD generally underestimated time durations, indicating a subjective slowing of time. This finding lends new insights into the experience of time in the range of seconds for adults with ADHD, as most existing studies have not examined durations in this range, and behavioral performance is often expressed in terms of absolute error (e.g., Pretus et al. 2020, Valko et al. 2010). These considerations highlight the novelty of our experimental paradigm, while making it more challenging to map onto previous work.

Second, there was no significant effect of group on timing precision as measured by the coefficient of variation. We compare accuracy and precision results to prior work below.

One prior study found that when estimating one-second intervals, the accuracy of adult participants with ADHD did not differ from controls (Mostert et al. 2015). Another study required adult participants with ADHD and controls to estimate the passage of one-minute intervals repeatedly within a four-minute session, and error values were calculated in a non-compounding manner. The participants with ADHD were less accurate than controls when they were not medicated, but performed similarly to controls when they were medicated (Wilson et al. 2013). Yet, another study paralleled our findings on accuracy more closely, but for much longer duration ranges; when tested on temporal reproduction on the order of several seconds (e.g., 12-60 s), young adults with ADHD produced shorter reproductions compared to controls (15 and 60 s intervals) and displayed greater reproduction errors (12, 45, and 60 s; Barkley et al. 2001). Similarly, one study tested ADHD participants from different age groups (children, adolescents, and adults) on temporal discrimination (staircase method by Levitt, 1971; durations: 1000-1300 ms), temporal production (durations: 2, 6, 12, 24, 36 and 48 s), and temporal reproduction (durations: 2, 6, 12, 24, 36 and 48 s). Across all age groups, individuals with ADHD displayed less sensitivity in temporal discrimination and underestimated durations in the temporal production task, and adolescents and adults underestimated durations in the reproduction task (Marx et al. 2010). The duration ranges in these two studies include much larger intervals than in our study, and underscore that the tendency to underestimate durations in ADHD may be a persistent pattern on broader time scales. Our results also align with common reports of individuals with ADHD experiencing “time blindness” - these individuals often struggle to be on time to work, school, or appointments, resulting from a belief that they have more time to get ready or commute than they actually do. A subjective slowing of time and pattern of underestimating intervals could give rise to these challenging experiences.

Our findings can also be compared to studies about timing in children and adolescents with ADHD. In one case, researchers tested children with ADHD (with and without reading difficulties) and controls within the age range of 6.4 to 11.9 years on temporal discrimination and

reproduction tasks (Toplak et al. 2003). The supra-second intervals included in the temporal reproduction test were 2000 and 6000 ms, and it was found that all children with ADHD displayed greater variability for the 2000 ms duration (no accuracy differences). Additionally, all children with ADHD were more variable in their estimates for both intervals, while only children with ADHD plus reading difficulties differed in accuracy for the 6000 ms duration. In another study, researchers tested children with ADHD and controls between the ages of 7 and 14 on a temporal discrimination task using intervals between 1000 and 1300 ms. Using the staircase method of discrimination (Levitt, 1971), they determined that children with ADHD required a greater difference between intervals to correctly discriminate them (Smith et al. 2002). These studies naturally have the caveat of being focused on children, further highlighting the need to conduct more studies on timing in adults with ADHD. However, taken together, these studies demonstrate that timing in ADHD remains a challenge from childhood to adulthood.

Third, when comparing timing performance between movement and hold conditions, neither group experienced a significant effect on accuracy (BP) or precision (CV). This finding was particularly surprising because it did not align with our prior findings highlighting the beneficial effect of movement on timing (Wiener et al. 2019). This previous study demonstrated a movement-related boost in timing precision across both temporal categorization and temporal reproduction paradigms. One potential explanation for the divergence from our current findings could lie in the different study parameters; in the current study, both movement conditions were experienced by every participant, whereas in the prior study, participants were randomly assigned to a movement or hold condition that were fixed throughout the entire experiment. It is possible that the benefit of duration is experienced throughout a longer context (i.e., a full experiment), and is counteracted by interleaving non-movement trials every 28 or 56 trials, as in this experiment.

Fourth, it was somewhat surprising to find no difference in movement distances between groups for the movement trials. ADHD is often accompanied by hyperactivity and fidgeting

behavior, which could be expected to translate to elevated movement in this task. However, the movement component of the task was required and it could be that the intrinsic and spontaneous nature of fidgeting does not necessarily map onto an instructed motor task. Fidgeting has been previously identified as a potential avenue to regulate arousal in individuals with ADHD (Zentall, 1975; Fassbender & Schweitzer, 2006), and has even been shown to improve cognitive control for children with ADHD (Hartanto et al. 2016). Thus, it would be interesting to study the effects of uncued, intrinsic fidgeting on timing performance.

Taken together, our study demonstrates a robust difference in timing accuracy, specifically a shortening of time perception, for adults with ADHD compared to healthy controls. These results have not yet been shown for an adult ADHD sample using the duration range of a few seconds, and adds a new perspective to existing literature. While effects of movement were not observed on timing performance, we suggest that studying the effect of movement over a longer experimental context may lead to more interesting insights. Further, our sample size was relatively small for a study comparing ADHD and control groups, and it would be beneficial to aim for a higher sample size in the future. Regardless of these limitations, our study contributes to the larger understanding of adult ADHD and calls for further research into the timing differences and challenges faced by these individuals, as well as strategies to assist them in real-world timing tasks to improve their quality of life.

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