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**Time on your hands: Perceived duration of sensory events is biased towards
concurrent actions**

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Abstract

Perceptual systems must rapidly generate accurate representations of the world from sensory inputs that are corrupted by internal and external noise. We can typically obtain more veridical representations by integrating information from multiple channels, but this integration can lead to biases when inputs are, in fact, not from the same source. While a considerable amount is known about how different sources of information are combined to influence *what* we perceive, it is not known whether temporal features are combined. It is vital to address this question given the divergent predictions made by different models of cue combination and time perception concerning the plausibility of crossmodal temporal integration, and the implications that such integration would have for research programmes in action control and social cognition. Here we present four experiments investigating the influence of movement duration on the perceived duration of an auditory tone. Participants either explicitly (Experiments 1-2) or implicitly (Experiments 3-4) produced hand movements of shorter or longer durations, while judging the duration of a concurrently presented tone (500-950 ms in duration). Across all experiments, judgments of tone duration were attracted towards the duration of executed movements (i.e., tones were perceived to be longer when executing a movement of longer duration). Our results demonstrate that temporal information associated with movement biases perceived auditory duration, placing important constraints on theories modelling cue integration for state estimation, as well as models of time perception, action control and social cognition.

Keywords: Time Perception; Cue Combination; Sensorimotor Integration

Introduction

It has long been appreciated that our perceptual systems face a considerable challenge in rapidly generating accurate representations of the world, especially when these sensory inputs are corrupted by inherent internal and external noise. We may obtain a more veridical representation by integrating information from multiple channels, either across sensory modalities or between motor and perceptual representations. A multitude of studies demonstrate that we integrate across concurrent visual and tactile events, such that visual events facilitate tactile processing from the same point in space (Spence, Nicholls, Gillespie & Driver, 1998) and vice versa (Kennett, Eimer, Spence & Driver, 2001), and vision of a body part improves tactile discrimination thresholds (Kennett, Taylor-Clarke & Haggard, 2001; Taylor-Clarke, Kennett & Haggard, 2002). A range of evidence has been found for similar integration effects involving auditory information (Alais & Burr, 2004) and across action and perception (Schütz-Bosbach & Prinz, 2007). While this integration is typically beneficial given that concurrent events often have a common source, it can lead to biases when the inputs come from separate sources. For example, in the 'McGurk Effect' (McGurk & Macdonald, 1976), the listener perceives 'da' when presented with the sound 'ba' while observing the speaker say 'ga'; the percept is of a syllable that integrates acoustic and visual cues indicating the place of articulation. Additionally, actions bias perception across a range of settings. For instance, the perceived direction of an ambiguous display of moving dots is biased in favor of the direction of a concurrent hand rotation (Wohlschläger, 2000).

Cue integration is likely to be of paramount importance in sensorimotor coordination. Effective action control is only possible due to interactions between motor and sensory systems. We select actions based on their anticipated sensory outcomes (Greenwald, 1970; Hommel, Müsseler, Aschersleben, & Prinz, 2001), and when incongruent sensory signals are experienced, corrective adjustments are made to ensure successful execution. For example, when picking up a cup of tea, the motor commands result in the sight of grasping and lifting, and cutaneous stimulation on the fingertips. If the actual feedback differs from the anticipated sensory outcomes, rapid corrective actions can be executed to avoid spillage. It is essential that we represent not only the nature of our action outcomes (e.g., sight of lifting; 'what' information), but also crucially, the onset and duration of these outcomes (e.g., the duration of the lifting

interval; 'when' information). For example, lifting the teacup from a saucer requires an anticipatory response to maintain postural stability (Diedrichsen, Verstynen, Hon, Lehman, & Ivry, 2003; Dufossé, Hugon, & Massion, 1985). Similarly, anticipating the duration of the lift phase is essential for coordinating hand and mouth gestures, and when shaking someone's hand, contact must be made for an appropriate length of time – neither too long, nor too short - to convey the intended social message.

Systematic temporal biases reflect the integration of action and perception. Studies investigating 'intentional binding' reveal that when an action's effect occurs at a delay after execution, the two events are perceived to occur closer in time (i.e., such that actions are perceived to occur *later* and effects *earlier*; Haggard, Clark, & Kalogeras, 2002; Moore & Obhi, 2012). In a similar vein, motor-sensory temporal recalibration tasks demonstrate that participants adapt to short delays between actions and their effects, such that after an exposure period, events presented with a physical delay are perceived to be synchronous with movement (Stetson, Cui, Montague, & Eagleman, 2006; Yarrow, Sverdrup-Stueland, Roseboom & Arnold, 2013). While these studies show that cue integration influences the perceived timing of the events, they do not address whether temporal features themselves are integrated. In other words, the current literature does not inform whether temporal features of one event influence the perceived duration of another.

It could be anticipated that cue integration is comparable for 'what' and 'when' information. Cue integration is often thought to reflect the influence of expectations on perception: We expect to hear a syllable that matches information presented in the visual channel, and we predict that a sensory event will be congruent with a concurrently executed action. Under this account, the percept emerges through the resolution of the predictions and sensory input (Summerfield & Egner, 2009). Extended to the temporal domain, we would expect the integration of temporal signals given that they often predict each other. For example, when musicians produce an action (e.g., bowing a cello), the generated percepts (e.g., observed movement, musical notes) typically last for a period of time similar to the movement. Indeed, under any model of cue integration, combining concurrently presented temporal signals is likely to aid perception as they will often have been produced by the same source. It is vital to address this question given the implications that such integration would have for research programmes in action control and

social cognition (e.g., Schütz-Bosbach & Prinz, 2007), and the divergent predictions made by different models of time perception concerning the plausibility of crossmodal temporal integration. For example, such cue integration is consistent with predictions made by dedicated models of time perception (Ivry, 1996) but not models that are modality-specific (Buonomano, 2000; see General Discussion for a more detailed exposition, as well as implications for other models).

In the current studies, we therefore examine whether temporal cue integration is observed between action and perception when the signals arise from different events. In particular, we ask if the perceived duration of a tone is influenced by the duration of a concurrent movement, even when the durations are independent. On each trial, the participant performed a movement of variable duration. The onset of the movement triggered a tone, but the duration of the tone was independent of the movement duration. The key question was whether participants' judgments of tone duration were influenced by the duration of the movement. We predicted that temporal cues would be combined such that auditory duration perception would be biased towards that of the executed action duration, similar to that observed with 'what' cues (e.g., McGurk & McDonald, 1976; Wohlschläger, 2000). In other words, participants would be more likely to perceive tones as longer when concurrently performing a long, rather than short, action.

Experiment 1

In Experiment 1, participants were instructed to execute short or long movements while judging the duration of a concurrently presented tone. Our focus is on whether the perceived duration of the tone is influenced by the duration of the movement.

Method

Participants

Twenty participants were recruited from Birkbeck, University of London and paid a small honorarium. The data from four participants were excluded because their performance was highly variable, yielding

psychometric functions that could not be modelled effectively in at least one condition (see below). These exclusions resulted in a final sample size of 16 (9 female, mean age = 24 years, SD = 4.85). This sample size was determined a priori to provide at least 90% power for detecting an effect of the experimental manipulations, estimated on the basis of pilot testing (we note that with this sample size and level of sensitivity, we are limited in terms of the precision of the actual measurements). The same target sample size was employed in Experiments 2-4.

All participants reported normal vision and hearing, no history of neurological or psychiatric illness, and were naïve to the purpose of the study. The experiment was performed with local ethical committee approval in accordance with the ethical standards laid down in the 1964 Declaration of Helsinki.

Procedure and Stimuli

The participant was seated approximately 55 cm away from a computer monitor inside a dimly lit cubicle, with their right hand positioned over a keypad placed in front of the body midline. A black screen prevented the participants from viewing their right hand. Perceptual judgments were made with the left hand on a separate keypad that was positioned to left of the screen covering the right hand. The experiment was run using the Cogent toolbox for MATLAB. All visual stimuli were presented against a black background on a CRT computer monitor (32 x 24 cm, 85 Hz, 21 DPI), while all auditory stimuli were presented over Sennheiser HD 201 headphones (81 dB).

The experiment began with a short block to train the participant to produce short and long duration movements. The participant depressed the response key with the index finger of their right hand, maintaining this position during the inter-trial interval. On each trial, an 'S' or 'L' was presented on the screen, indicating the required movement duration. The cue remained visible until the participant lifted her finger to initiate the movement. After the lift, the participant repressed the response key, attempting to match the criterion movement duration (<500 ms for short and >950 ms for long responses). The movement was modelled by the experimenter such that the finger moved smoothly to and from the apex of the lift. The training block consisted of 20 trials, ten short and ten long. Participants received auditory

feedback (100 Hz, 500 ms long) when the produced duration was outside the criterion for that trial. Each movement was followed by an inter-trial interval of 500 ms, at the end of which the next cue appeared.

In the main experimental blocks, the participant performed two, interleaved tasks: the movement task as described above and a duration discrimination task. The time course of the events for each trial is illustrated in Figure 1. The trial started with the presentation of the duration cue ('S' or 'L'). When the participant initiated her finger lift, the screen was blanked and the test tone was played. The duration of this tone was drawn from a set of seven durations, ranging from 500-950 ms (75 ms steps, all 500 Hz). At a variable delay after the participant returned her finger to the start position (1000-1500 ms), the reference tone of a fixed duration, 725 ms, was played (again 500 Hz). If the cued movement had been executed correctly, a response screen appeared instructing the participant to indicate which tone was longer. The tone judgments were indicated by a keypress with the left thumb, pressing the left key if the first tone was longer and the right key if the second tone was longer. If the movement duration was outside the criterion for that trial, an error message was displayed ('Too fast!' or 'Too slow!'). No perceptual judgments were obtained on these trials and the trial was repeated.

The participant completed eight practice trials of the concurrent movement/duration discrimination task. Test blocks were a minimum of 70 trials each (five of each target duration for each movement condition) and the trial order was randomized. There were two test blocks. Thus, the final data set consisted of 10 trials at each test tone duration in which the required movement duration was correctly produced.

When the experiment had been completed, participants were asked whether they had noticed anything about the tones, and in particular, anything of note about the second tone. None reported being aware that the reference tone was identical in duration on every trial (this same pattern was observed in all four experiments).

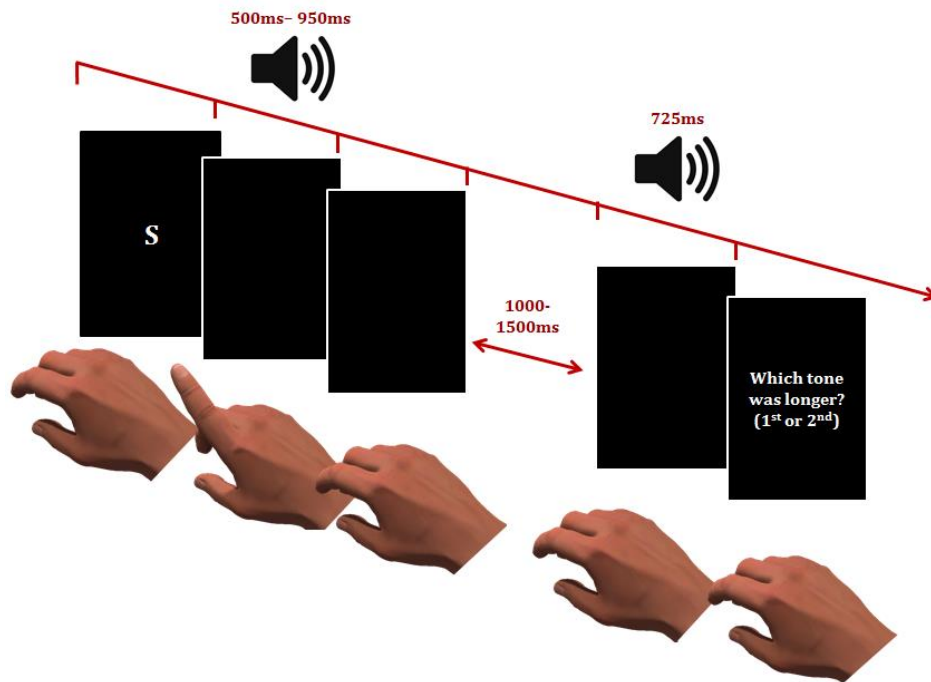


Figure 1: Time course of stimulus presentation and participant movements on a single test trial in Experiments 1 and 2.

To estimate psychometric functions, the perceptual judgments for each individual were modelled by fitting cumulative Gaussians, and associated pDev statistics were calculated to establish the goodness-of-fit for each function (Palamedes toolbox, Kingdom & Prins, 2009). This procedure was performed separately for the long and short response conditions. In each condition, bias was inferred from the point of subjective equivalence (PSE) and precision from the standard deviation of the Gaussian distribution that best fit the data (see Figure 2).

As noted above, four participants had an unacceptably poor fit ($pDev < 0.05$), or PSEs beyond the range of presented stimuli for at least one function, and were not included in the main analyses. However, as a secondary report for key analyses, we also note statistics based on data sets including most of these participants.

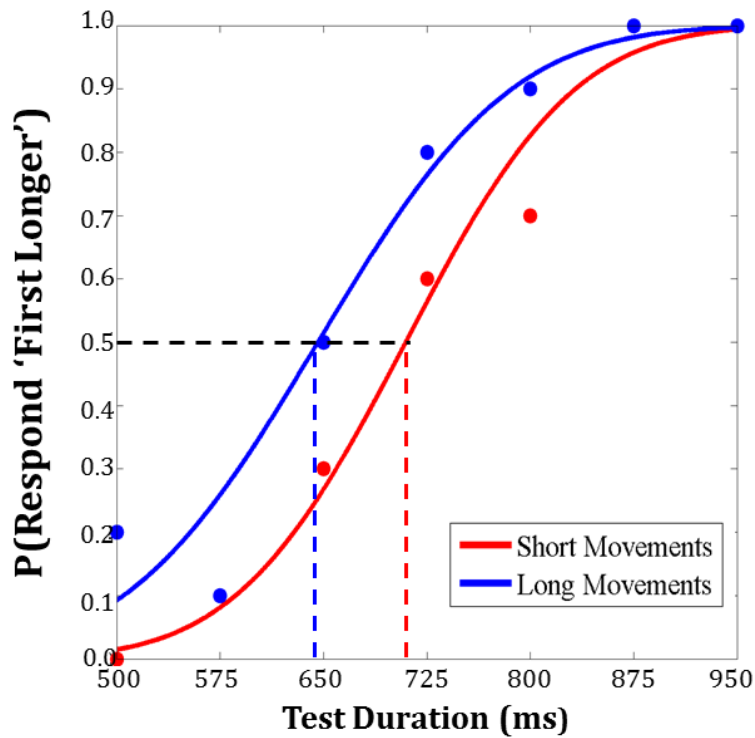


Figure 2: Illustration of how PSEs were calculated from cumulative Gaussians modelled to judgments in the short and long movement conditions. The PSE (dotted line) describes the point where participants judge the target and reference events to have equal duration. Please note the data points for the two conditions overlap for stimulus durations of 575 and 875 ms.

Results and Discussion

The participants had little difficulty producing movements of different durations in the two conditions. The mean number of movement errors was 7.7% (SEM = 1.9%). The mean duration of correct movements was 255.4 ms (SD = 105.9 ms) in the short condition, and 1577.5 ms (SD = 521.6 ms) in the long condition (Figure 3).

As can be seen in the example psychometric functions (Figure 2), participants were more likely to judge the target stimulus as longer on trials requiring a long duration movement. This bias results in lower PSE values for the long duration movement condition compared to the short duration movement condition (Figure 3), an effect that was highly significant ($t(15) = 7.82, p < .001, d = 2.21$). There were no differences between the two movement conditions in terms of the precision of the perceptual judgments

($t(15) = .678, p = 0.51$). The mean Weber fractions (precision/duration of the reference stimulus) were .65 (SEM = .09) and .70 (SEM = .09) in the Long and Short movement conditions, respectively.

We repeated this analysis, including three of the four participants who had been excluded because they did not meet the pDev and PSE range criteria; we still excluded one participant whose PSE in one condition deviated >10 SDs from the sample mean. This analysis revealed the same effect in PSEs ($t(18) = 6.92, p < .001$) with no difference in precision ($t(18) = 1.47, p = .160$; see Supplementary Figure 1).

These findings demonstrate a strong influence of movement duration on the perceived duration of a concurrently presented tone, suggesting that ‘when’ information biases perception in a similar way to ‘what’ information. This result may reflect the integration of motor and auditory temporal signals, a process that we might expect given that temporally contiguous events from different modalities typically come from the same source, and therefore last for a common duration.

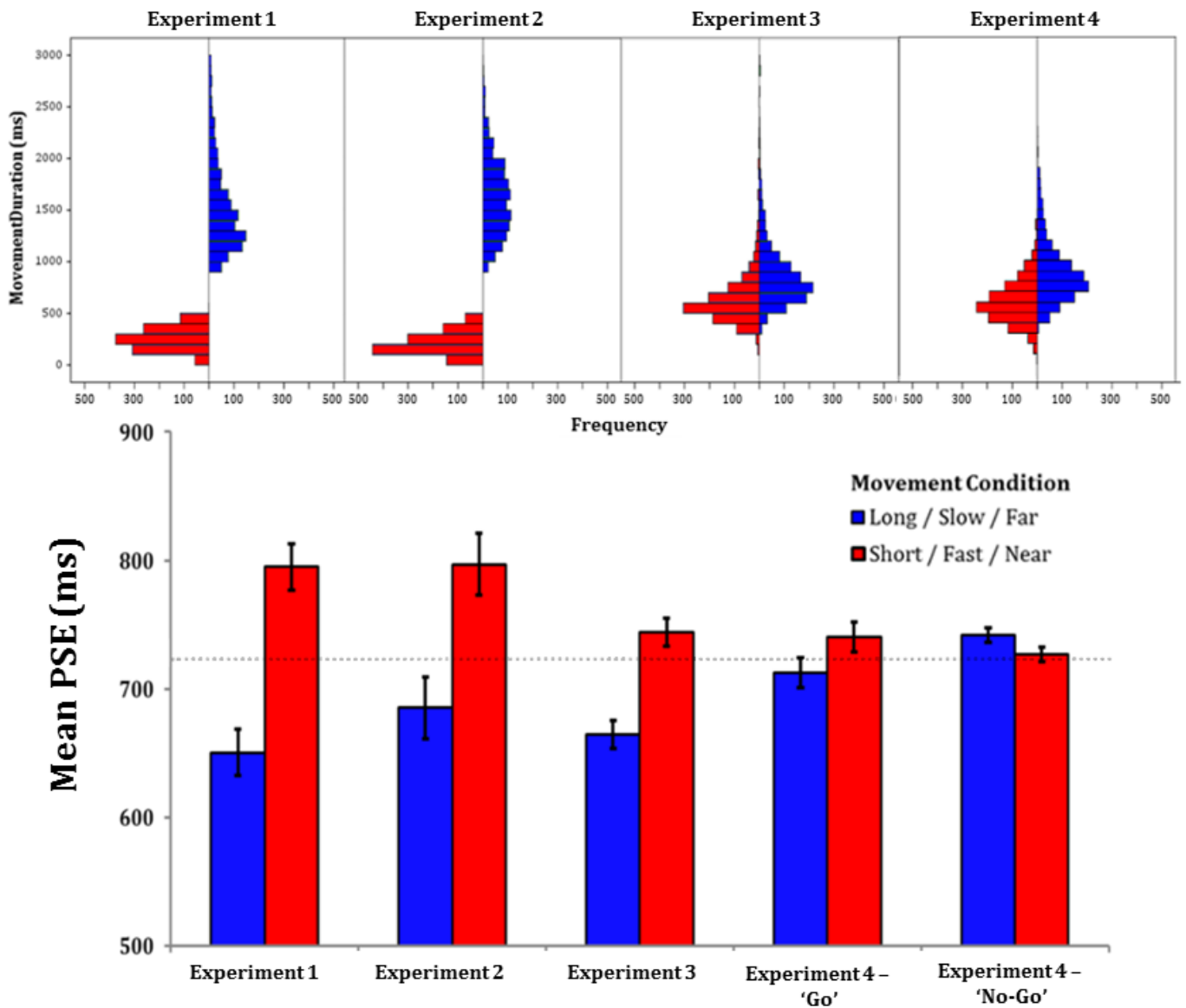


Figure 3: Top panels: Distribution of movement times across the conditions of Experiments 1 - 4 collapsed across all participants (who met the inclusion criteria). Bottom panel: Mean PSEs in the conditions across experiments. Note that lower PSEs indicate a bias to perceive the target stimulus as *longer*. Dotted line indicates the duration of the reference tone (725 ms). Error bars show 95% within-subject confidence intervals (Cousineau, 2005).

Experiment 2

We assume that the biases observed in Experiment 1 arise from the interaction of two temporal codes, one representing the duration of the movement, the other representing the duration of the tone. Alternatively, the interaction might arise at a linguistic level. For example, the movement conditions were described in terms of duration, and on each trial, the participant saw an explicit temporal cue, 'L' to indicate that they should produce a long duration movement and 'S' to indicate that they should produce a short duration movement. It is possible that the linguistic temporal labels introduced cross-talk between the two tasks and that these labels produced the observed biases, rather than temporal information associated with the movements themselves (Kornblum, Hasbroucq & Osman, 1990; Casasanto & Boroditsky, 2008; Klemfuss, Prinzmetal & Ivry, 2012).

To evaluate this common labelling hypothesis, we repeated the basic procedure of Experiment 1, but modified the manner in which the movement task was described and cued to reduce the linguistic overlap with the perceptual task. In Experiment 2, participants were instructed to vary the speed of their movements, executing 'fast' or 'slow' movements in response to on-screen cues ('F' and 'S', respectively). Cuing movements in this manner should reduce linguistic overlap. If the effect described in Experiment 1 is mediated by cross-talk introduced by shared 'long' and 'short' linguistic codes, we would expect the perceptual biases generated by movement to be abolished in Experiment 2.

Method

A new sample of 23 participants took part in Experiment 2. Eligibility criteria were identical to Experiment 1. The data from seven participants were excluded because their performance was highly variable, yielding psychometric functions that could not be modelled effectively in at least one condition. These exclusions resulted in 16 in the final sample (13 female, mean age = 22 years, SD = 3.53). The stimuli and procedure for Experiment 2 were identical to Experiment 1 with the following change: The participant was instructed to perform 'slow' and 'fast' movements, conditions that were cued with the letters 'S' and 'F', respectively. The criteria were identical to that of Experiment 1: 'fast' movements were required to be <500 ms in duration and 'slow' movements were required to be >950 ms in duration.

Results and Discussion

As in Experiment 1, the participants had little difficulty meeting the demands of the movement task. The mean durations were 213.4 ms (SD = 103.9 ms) in the short condition, and 1644.2 ms (SD = 503.9 ms) in the long condition (Figure 3). Movement errors occurred on 7.1 % (SEM = 2.1 %) of the trials.

The comparison of the PSEs on the duration perception task again revealed a highly significant effect ($t(15) = 4.56, p < .001, d = 1.76$). The PSEs were lower in the slow movement condition relative to the fast condition (see Figure 3). As in Experiment 1, there was no difference between the movement conditions in terms of precision ($t(15) = 1.89, p = .078$), with mean Weber fractions of .79 (SEM = .15) and .55 (SEM = .04) in the Slow and Fast conditions, respectively. We repeated these analyses, including the data from five of the seven participants who had been excluded on the pDev and PSE range criteria (the other two had a PSE estimate in one condition that deviated >10 SDs from the sample mean). In this expanded analysis, we again observed that the PSEs were lower in the slow movement condition ($t(20) = 4.31, p < .001$), with no difference in precision ($t(20) = .422, p = .677$).

In sum, the results of Experiment 2 show that tones are perceived to be longer when performing long movements, even when the lexical terms used to describe movement goals do not directly refer to duration.

Experiment 3

Experiment 2 allows us to reject an explanation of the bias based on the direct interaction of common lexical codes (i.e. 'long' or 'short'). However, we recognize that it remains possible that the effects are mediated at a linguistic level given that distinct instructions were provided for the 'long' and 'short' movement conditions, even if the labels were 'slow' and 'fast'. As such, the biases might arise from cross-talk between linguistic codes associated with the terms used for speed and duration. While adults understand time and speed as distinct dimensions, the lexical terms for time and speed are related. Moreover, young children tend to confuse these dimensions. Interestingly, these confusions reflect the

opposite mappings to those defined by Newtonian mechanics: For example, faster moving objects are erroneously judged to move for longer periods of time (Siegler & Richards, 1979). As such, if the effect observed in Experiment 2 was lexically-mediated we may have predicted the opposite pattern i.e., longer duration percepts on fast movement trials.

Nonetheless, concerns about lexical mediation can be more directly addressed by removing the labels entirely from the movement task. To this end, we designed a new task for Experiment 3 in which we elicited movements of varying duration by implicitly manipulating the other dimension that can covary with movement duration, movement distance (Fitts, 1954; note that movement duration must of course always covary with either distance, speed, or both). We used a simple task in which participants reached to a visual target that could appear at different locations on the display. By varying the position of the target, we could partition the movements into 'short' and 'long', and ask if the perceptual judgments differed between the two conditions. This method has the important advantage that the instructions are the same for both conditions ('reach to the target'), reducing the likelihood that effects are lexically-mediated. If we find a similar biasing effect to that observed in Experiments 1 and 2, it seems more reasonable to attribute the effect to action duration rather than the explicit framing of the movement task.

Method

Participants

A new sample of 21 participants were recruited from Birkbeck, University of London and paid a small honorarium for participation. Eligibility criteria were identical to Experiments 1 and 2. The data from four participants were excluded because their performance was highly variable, yielding psychometric functions that could not be modelled effectively in at least one condition. An additional participant was excluded as movement time analysis (see below) revealed no differences in movement durations between Near and Far target conditions ($t = .016, p = .988$). These exclusions resulted in a final sample of 16 (7 female, mean age = 21.4 years, SD = 2.8).

Procedure and Stimuli

The visual targets were displayed on a vertically-oriented computer monitor positioned in front of the participant (Figure 4). Vision of the arm was occluded by the black screen. Movement position was recorded by a small motion tracker (Leap Motion Controller using the Matleap MATLAB interface, sampling rate = 20 Hz - note that this rate was selected during piloting to eliminate potential interference with the dynamics of stimulus presentation, yet still establish static hand position within 50 ms of arrival at the target location) which recorded the center of the palm in 3D space.

Each trial began with presentation of cursor feedback (white dot, 0.2° visual angle) corresponding to the participant's palm position. This allowed her to verify that her hand was at a central starting position. After 2000 ms, a blue target circle (3 cm in diameter, $\sim 3^\circ$ visual angle) was presented on the display. The location of the target was constrained to fall within one of two 45° wedges about the horizontal meridian, with half of the targets appearing to the left and half to the right. The participant reached to the target by moving her hand above the table surface (without making contact; see Figure 4). The instructions emphasized accuracy over speed, with participants told to execute a single smooth movement, without attempting corrections (given there was no movement feedback, corrections would have been infrequent). They were to keep the hand at the final location until the end of the trial. Movement time was recorded as the interval between movement onset (>1 cm change from starting position) and offset (movement velocity <40 mm/s; both criteria were set during piloting to maximize the identification of start-stop movement periods while minimizing false alarms). If the participant failed to complete the movement within 3000 ms of the target onset, they received error feedback and the trial was repeated. After 5 s, the screen was blanked, signaling the end of the trial. This was followed by a 2 s ITI, during which participants were required to move back to the central starting position.

The test session began with two practice blocks (10 trials each). In the first practice block, cursor feedback was continuously provided to familiarize the participants with the reaching task. This block was followed by a second practice block in which the cursor was only visible for 1000 ms at the start of each trial (also the case in the main task). Error feedback was provided if the final hand position was outside the target circle. The error feedback was a red dot (0.2°), indicating the position of their palm.

The test block consisted of 168 trials in which the participants concurrently performed the reaching and tone duration tasks. The location of the reach targets was manipulated such that 70 reaches were to targets positioned 5 – 8 cm from the start location (Near) and 70 reaches were to targets positioned 15 – 18 cm from the start location (Far). Pilot testing indicated that with these ranges there would be a measurable difference in mean movement time. To prevent participants from becoming aware of the clusters of near and far targets, we also included an additional 28 trials in which the targets were 10 – 13 cm from the start location (intermediate).

A tone was presented as soon as the participant initiated the reaching movement. As in Experiments 1 and 2, the duration of this tone varied between 500 and 950 ms (75 ms steps, all 500 Hz). At a random delay after the termination of the test tone (1500 – 2000 ms) a second reference tone was presented (725 ms). Participants were instructed to complete their movements before the onset of the reference tone. The participant was considered to have missed the target if they had not reached the target area within 3000 ms of movement initiation. If the reach had landed in the target zone within this 3000 ms window, the participant was required to judge which of the tones was longer, and to move back to the central start position after making their judgment. If the target was missed, the participant received error feedback (red cursor indicating hand position) and the trial was repeated at the end of the experiment. Each test tone was presented 24 times; 10 times on trials with Near targets, 10 times on trials with Far targets, and 4 times on trials in which the target was at an intermediate location. Trials were randomized and breaks were taken every 20 trials. Psychometric functions were modelled to responses in Near and Far trials as in Experiments 1 and 2.

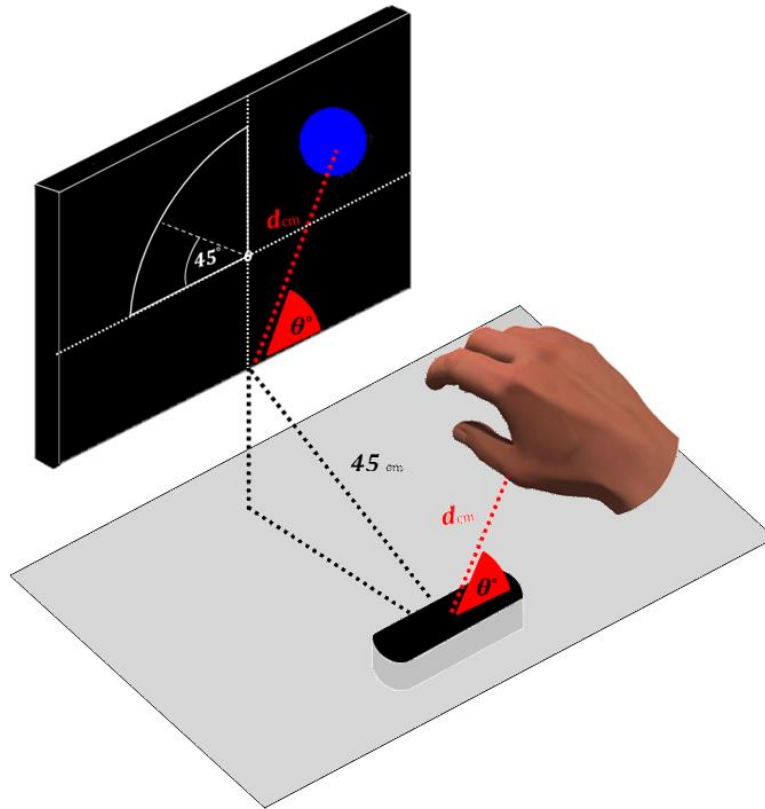


Figure 4: Illustration of set up in Experiment 3 and 4. A blue circle, presented on a vertically-oriented monitor, indicated the target location (defined by distance d and angle θ). Target locations were limited to the upper left and right quadrants of space, presented at a random angle from 0-45° with respect to the horizontal meridian (shown in white). This generated two discontinuous wedges (one left – illustrated, one right) in which the targets could appear. Reaches were made by moving the hand above and along the horizontal surface of a table where the motion tracker was placed. Vision of the hand was occluded by a black screen. On ‘No-Go’ trials in Experiment 4, the targets were presented, but participants were required to remain at the central starting position.

Results and Discussion

Despite the absence of visual feedback, participants were accurate in terminating their movements in the target region. The mean number of errors was 11.5 % (SEM = 2.3 %). Participants were also successful in terminating movements before the reference tone began (mean accuracy = 99.5 %, SEM = 0.3 %). As can be seen in Figure 3, the movement time distributions showed considerable overlap. Nonetheless, the means of the two distributions were displaced, indicating that movement time increased with movement amplitude. The mean movement times in Near and Far conditions were 619.0 ms (SD = 267.9 ms) and 859.6 ms (SD = 346.1 ms) respectively. To ensure that our distance manipulation was successful for each individual, we compared the MT distributions for each participant with a t-test. These tests were all

highly significant (all $t_s > 2.87$, all $p_s < .005$; bar one excluded participant – see above). Thus, our manipulation of distance was effective in creating different timings for the Near and Far conditions, even though the temporal difference was much smaller than in Experiments 1 and 2.

Turning to the perceptual judgments, a comparison of PSEs on the duration perception task revealed significant differences between the movement conditions - $t(15) = 7.16$, $p < .001$, $d = 1.18$. PSEs were significantly lower in the Far (long) target condition relative to Near (short) target condition (see Figure 3), suggesting that tones are perceived to be longer following reaches to more distant targets. No significant differences were found in judgment precision - $t(15) = 1.78$, $p = .096$ - with mean Weber fractions of .54 (SEM = .06) and .46 (SEM = .04) in the Far and Near conditions, respectively. The analysis was repeated with the data from all 21 participants, including the five who did not meet pDev and PSE range criteria. As in the main analyses, there was a significant effect of PSE ($t(20) = 3.69$, $p = .001$) with no difference in precision ($t(20) = .797$, $p = .435$).

In line with the findings of Experiments 1 and 2, these results suggest that the duration of executed movements influences the perceived duration of auditory events. The effect is especially striking here given that the duration differences in movement time were an emergent property of target distance, and were not explicitly marked by the instructions.

Experiment 4

Experiment 3 allows us to reject the hypothesis that the bias observed from movement on perceived duration is driven by explicit labels attached to the movements. However, by exploiting the coupling between target eccentricity and movement duration, we introduced a different confound: Namely, when participants produced reaches with longer durations, they also observed targets presented at greater eccentricities from the center of the screen. It is therefore possible that the bias seen in Experiment 3 is driven by the observation of small and large visual eccentricities, rather than by the duration of the executed movements.

To evaluate this hypothesis, we used the task employed in Experiment 3, but added a Go/No-Go manipulation. On each trial, a target was presented, but movements were only required if the color of the cursor representing the position of the participant's initial palm position was green (Go trials); No-Go trials were signaled when the cursor was red. If the bias is driven by the perceptual difference between near and far targets, then we should observe similar biases on Go and No-Go trials. Conversely, if the bias is driven by the duration of the movements, it should only be observed on Go trials.

We also used Experiment 4 to address a second methodological issue in Experiments 1-3. In those experiments, the participants always executed their movements during the first tone interval and this was followed by the reference tone interval. We assume the observed interaction between action and perception is not dependent on this feature. Nonetheless, we reversed the order of the reference and target tones in Experiment 4 such that the reference tone was presented first, followed by the test tone and movement. We predicted that the bias would persist under this condition.

Method

Participants

A new sample of 20 participants were recruited from Birkbeck, University of London and paid a small honorarium for participation. The data from four participants were excluded because their performance yielded psychometric functions that could not be modelled effectively in at least one condition. These exclusions resulted in a final sample of 16 (10 female, mean age = 26.1 years, SD = 5.3).

Procedure and Stimuli

The procedure and stimuli used in Experiment 4 were identical to Experiment 3 with the following changes. Like in Experiment 3, each trial began with the presentation of cursor feedback corresponding to the participant's palm position. In Experiment 4 the color of this cursor indicated the movement task for the forthcoming trial. On Go trials the cursor was green, indicating that the participant would be expected to reach to the target. On No-Go trials, the cursor was red and participants were instructed to keep their hand in the central starting position. After 2000 ms, the 725 ms reference tone was played. At

a random delay after the termination of the reference tone (1500 – 2000 ms), a blue target circle was presented. On Go trials, this served as the imperative and movement initiation triggered the presentation of the test tone. On No-Go trials the test tone was presented 500 ms after target onset. This timing was selected to approximate the interval between the target and tone onsets in the Go conditions (anticipated average RT). By using a fixed interval here, the onset of the tone was equally predictable in both conditions. Criteria for successful movements on Go trials were identical to Experiment 3, based on the terminal position of the hand with respect to the target. Movements greater than 5 cm from the start position (in any direction) were considered errors on No-Go trials. We opted to use a liberal criterion here since the participants' hands tended to drift from the start position given that the hand was suspended in mid-air, and pilot testing indicated that the criterion was sufficient to detect erroneous reaches.

The test block consisted of 336 trials. Each test tone was presented 48 times: 20 times on trials with Near targets, 20 times on trials with Far targets and 8 times on trials in which the target was at an intermediate location. Half of the trials were Go trials and the other half were No-Go trials. All trial types were randomized. Psychometric functions were modelled separately for the four conditions, Near-Go, Far-Go, Near-No-Go, Far-No-Go. Breaks were provided every 30 trials.

Results and Discussion

Participants were accurate in performing the reaching movements on Go trials, with errors occurring on an average of 9.6 % (SEM = 1.35) of trials. As can be seen from Figure 3, the movement time distributions for the Near and Far conditions on Go trials showed considerable overlap. Nonetheless the means of the two distributions were displaced, indicating again that movement time increased with movement amplitude. The mean movement times for Near and Far Go trials were 583.3 ms (SD = 210.0 ms) and 872.9 ms (SD = 298.9 ms). For each participant, movement time distributions were compared with a t-test. These tests were all highly significant (all $t_s > 5.98$, all $p_s < .001$). Thus, the manipulation of distance was effective in creating different timings for the Near and Far Go conditions, similar to that observed in Experiment 3.

The PSEs (now derived from cumulative Gaussians modeled to P(respond 'second longer') against test duration) were analyzed using a 2 x 2 repeated measures ANOVA, with factors of target distance (Near, Far) and task (Go, No-Go). This analysis found no effect of task ($p = .632$) or target distance ($p = .385$), but a significant interaction between these factors, $F(1,15) = 11.27, p = .004, \eta^2 = .429$. Simple effects analyses revealed a cross-over interaction: In the Go condition, PSEs were lower for Far targets compared to Near targets, $t(15) = 2.29, p = .037, d = .444$, while in the No-Go conditions, PSEs were lower for Near targets than Far targets, $t(15) = 2.69, p = .017, d = .329$. Therefore, as in the previous experiments, the tones were perceived to be longer following reaches to more distant targets.

Unexpectedly, the opposite effect was observed in the No-Go condition, with short target locations associated with longer perceived tone durations. This reverse effect may reflect the inhibition of movement on these trials. Previous work has shown that withholding movements can bias perception away from associated spatial features (e.g., when planning a leftward movement, stimuli appearing during the preparatory period are biased to appear rightwards from their actual position; Kirsch & Kunde, 2014). Our reversed effect in the No-Go condition could reflect an analogous effect on temporal features, where inhibiting movements that would have a particular duration biases perception away from intervals associated with those actions. We note that the bias observed on Go trials in Experiment 4 had a reduced effect size, relative to that observed in Experiments 1-3. We speculate this could be due to residual inhibition from No-Go trials.

Judgment precision was also analyzed using the same factorial ANOVA. This analysis revealed a main effect of task, $F(1,15) = 16.18, p = .001, \eta^2 = .519$, with better discrimination performance in No-Go conditions relative to Go conditions. This effect is expected given that participants are simultaneously performing a motor task when judging the tones in the Go, but not No-Go condition. No other effects were significant (all $p > .058$). Mean Weber fractions of .41 (SEM = .04) and .50 (SEM = .07) were obtained for Near and Far trials in the Go condition, while Weber fractions of .26 (SEM = .02) and .31 (SEM = .03) were obtained for Near and Far trials in the No-Go condition. The lower Weber fractions in the No-Go condition are comparable to those typically observed in the time perception literature with inexperienced participants, suggesting that the high Weber fractions in Experiments 1-3 (and the Go

condition of this experiment) reflect a dual-task cost in performance. Although it is possible that the cost could arise from the sharing of similar (temporal) representations between the two tasks, a more likely explanation is that there is some capacity-sharing between the tone judgment and target reaching tasks. Given that the stimuli and responses for the two tasks were temporally segregated (i.e. tones for the judgment task were only presented once response for the reaching task had been initiated), we speculate that this cost reflects sharing at a more central processing stage (Tombu & Jolicœur, 2003) rather than a competition at perceptual or response levels.

We repeated this analysis, including three participants who did not meet pDev and PSE range criteria (one remained excluded as the PSE in one condition deviated >10 SDs from the sample mean). These analyses revealed the same interaction between task and target distance for the PSE data, $F(1,18) = 14.3$, $p = .001$. As in the main analysis, this interaction was driven by lower PSEs for Far targets than Near targets in the Go condition, $t(18) = 2.68$, $p = .015$, and the opposite pattern in the No-Go condition, $t(18) = 2.20$, $p = .041$. The precision analysis also again revealed a main effect of task, $F(1,18) = 14.2$, $p = .001$.

In line with Experiments 1-3, the results of Experiment 4 indicate that the duration of an executed movement influences the perceived duration of concurrent auditory events. Importantly, the fact that this bias was absent when participants observed targets but were not required to move underscores that the effect is driven by the properties of executed movements rather than spatial properties of the target.

Cross-experiment Analysis

It is noteworthy that the MT distributions in Experiments 3 and 4 showed considerable overlap, whereas those in Experiments 1 and 2 were non-overlapping (by definition) and quite distinct (see Figure 3). We performed a post-hoc, cross-experiment analysis to ask if the size of the perceptual biasing effect was related to the size of the difference in the movement times. We first compared the movement time differences for the four experiments. For this analysis, we computed the difference between the mean for

the longer movement duration and the mean for the shorter movement duration for each participant, and then entered these scores into a one-way ANOVA with the factor experiment. There was a significant effect, $F(3,60) = 86.25, p < .001, \eta^2 = .812$, and post-hoc tests confirmed that the difference score was smaller in Experiments 3 and 4 compared to either Experiment 1 ($t(30) = 9.60, p < .001, d = 3.39$; $t(30) = 8.56, p < .001, d = 3.03$ respectively) or Experiment 2 ($t(30) = 17.44, p < .001, d = 6.17$; $t(30) = 14.15, p < .001, d = 5.00$, respectively). The comparison of Experiments 1 and 2 was not significant ($t(30) = 0.85, p = .403$), nor was the comparison of Experiments 3 and 4 ($t(30) = .926, p = .362$).

Given the above result, we pooled the participants into two groups, one formed by the participants from Experiments 1 and 2, and the other formed by the participants from Experiments 3 and 4. We then compared the magnitude of the PSE differences (Exp 1 and 2: short vs long or fast vs slow) of the first pooled group to the shifts observed for the participants in the second pooled group (Experiments 3 and 4: near vs far). This analysis revealed a significantly smaller effect of movement duration on PSE difference scores in Experiment 3 and 4 compared to Experiments 1 and 2, $t(62) = 4.14, p < .001, d = 1.04$. Thus, the size of the biasing effect on perceived duration of the tones was related to the size of the temporal difference in movement time, although we acknowledge that there are substantive methodological differences between the two groups.

General Discussion

The four experiments presented here demonstrate that auditory duration judgments are strongly biased by the duration of executed movements. In Experiments 1 and 2, the participants were asked to perform two concurrent temporal tasks, where they were instructed to regulate the duration (Exp. 1) or speed (Exp. 2) of a movement. In these experiments, we observed a strong biasing effect of movement duration on the perceptual judgments, with PSE differences of over 100 ms between the short/fast and long/slow movement conditions. We eliminated explicit temporal requirements from the movement task in Experiments 3 and 4, using an amplitude manipulation as a tool to elicit duration differences. Even under

this condition, we still observed an effect of action duration on perceived duration, although the effect was attenuated compared to Experiments 1 and 2. Taken together, the results demonstrate a novel interaction of temporal information between action and perception, even when the temporal cues are associated with distinct events.

Powerful demonstrations such as spatial ventriloquism (Alais & Burr, 2004) or the McGurk effect (McGurk & Macdonald, 1976) illustrate that our perception of stimulus features such as location or identity are determined by a combination of signals across modalities. The present results suggest that our perception of 'when' information is subject to similar cross-modal influences as that previously described for 'what' information. Cross-modal integration is assumed to promote a more veridical representation of our sensory environment by integrating information from multiple channels (Ernst & Banks, 2002). This integration is typically beneficial given that contiguous events usually have a common source, and in the time domain therefore last for comparable durations (e.g., speech gestures). Of course the converse of this advantage is that, when contiguous events are uncorrelated as in the present study, cross-modal integration will result in a distorted percept.

Interactions between perception and action in the temporal domain

Our results are particularly interesting in demonstrating temporal cross-talk between sensory and motor domains given the importance of cue integration for action control. Previous experiments have established that action execution influences 'what' we perceive. Ambiguous dot motion is perceived to move in the same direction as a concurrent hand movement (Wohlschläger, 2000), and trained pianists perceive ambiguous rising/falling pitch sequences in a direction consistent with a sequence of executed keypresses (Repp & Knoblich, 2007). Actions can also bias the perceived timing of sensory events. For example, participants judge tactile or visual events that are congruent with their executed actions (i.e., stimulation applied to a moving effector or observation of a moving effector) to have longer durations than incongruent events (Press, Berlot, Bird, Ivry, & Cook, 2014) and a delayed sound is perceived as closer in time to a keypress when it reliably follows the action (Haggard, Clark, & Kalogeras, 2002). The present findings extend this literature by showing that temporal features of action influence the

perceived duration of sensory events. Models of sensorimotor integration (e.g. Schütz-Bosbach & Prinz, 2007), both for explaining action control and perception, need to accommodate these interactions between sensory and motor timing.

Interestingly, models of sensorimotor integration are often employed to explain how we control our own actions and perceive the actions of others, but also to explicate our smooth interactions with others (Schütz-Bosbach & Prinz, 2007; Wolpert, Doya, & Kawato, 2003). While much of this work has focused on the goal or intention of the actions produced by others, it is also important that we predict and perceive the temporal features of these actions to make accurate inferences about their mental and affective states. For example, a reciprocated smile that is briefer than our own may be indicative of lower sincerity or awkwardness (Krumhuber & Kappas, 2005). The present results suggest that we are biased to perceive sensory effects as lasting for similar durations to our actions; therefore, motor-sensory cross-talk may actually cause us to perceive others' reactions as more temporally imitative, and thus may promote rapport, trust and pro-sociality even in the absence of veridical imitation of these temporal features (Ashton-James, van Baaren, Chartrand, Decety, & Karremans, 2007; Chartrand & Bargh, 1999; Thelen, Dollinger, & Roberts, 1975; van Baaren, Holland, Steenaert, & van Knippenberg, 2003).

Mechanistic accounts of the interaction between temporal properties of movement and perception

Our findings relate to, and may shed light upon, a number of issues in the time perception literature. There is ongoing debate concerning whether time perception depends on general mechanisms dedicated to representing time across modalities, or whether it arises as an intrinsic property of individual modality-specific networks (Ivry & Schlerf, 2008). For example, the cerebellar timing hypothesis, one instantiation of a dedicated model, suggests that duration information utilized for timed action and perception is represented in the cerebellum. These models contrast with modality-specific theories, such as state-dependent network models, which suggest that temporal perception depends upon neuronal dynamics within modality-specific processing regions (Buonomano, 2000). Importantly, under these modality-specific models, temporal representations in different modalities are not thought to interact. The finding that action duration biases the perceived duration of concurrent tones provides support for a

modality-general framework, whereby corresponding duration representations in different modalities can be related (Ivry & Schlerf, 2008).

Cross-talk between motor and sensory representations of time may also be useful for understanding why the motor system is involved in representing temporal features of the environment, even in the absence of movement. For example, fMRI studies implicate regions of the supplementary motor area in duration judgments, and ventrolateral premotor cortex when representing temporal regularities in sequences of arbitrary visual or auditory events in the absence of any requirement to act upon them (Schubotz, 2007; Schubotz & von Cramon, 2004; Schubotz, von Cramon, & Lohmann, 2003). Causal contributions of motor structures have been confirmed by the deficits seen in patients with premotor or cerebellar lesions (Ivry & Keele, 1989; Schubotz, Sakreida, Tittgemeyer, & von Cramon, 2004). These motor contributions may reflect, at least partly, the operation of similar mechanisms to those used during action. For example, correlated activation of sensory and motor representations will result in re-activation of the motor units when the sensory events are subsequently presented alone (Rescorla & Wagner, 1972; see also Cook, Bird, Catmur, Press, & Heyes, 2014; under such a learning account, one would also expect that contributions will be greater when presented with sensory events that are typically more highly correlated with action; for example, tactile and visual feedback may more commonly result from action compared to auditory feedback). One might speculate that a functional contribution of the motor system in these 'passive' settings pertains to persistent recalibration of noisy representations.

A pressing question for future work concerns how to characterize the temporal codes that underlie the observed interaction between movement and auditory duration. Our findings are consistent with Bayesian cue combination frameworks where different estimates of physical metrics (e.g. 1083 ms and 978 ms) are combined across modalities (Ernst & Banks, 2002; Alais & Burr, 2004), and may suggest that such cue combination models must be extended to incorporate temporal integration. By this view, there are two representations of physical time on each trial, one encoding the movement duration and one encoding the tone duration, and these representations are combined in a weighted fashion according to the reliability of the estimates (Ernst & Banks, 2002). A related account, that of the 'central tendency effect', suggests that learned contexts cause perceptual judgments to become attracted towards expected

intervals (Shi, Church, & Meck, 2014). A movement shorter than the tone duration will thereby exert a biasing effect to hear the tone as shorter than it actually is; the opposite will occur when the movement is longer than the tone duration. These cue integration models, based on the interaction of representations that are isomorphic in some manner to the real time properties of the movements, can account for the effects observed in Experiments 1 and 2. They would also be consistent with the fact that the biasing effects were attenuated in Experiments 3 and 4 given that there was a much smaller difference in the MT distributions between the two movement conditions (relative to Experiments 1 and 2). As cue combination models suggest the resultant perceptual estimate is a weighted average of the two internal signals, such models would predict attenuated perceptual biases when motor durations are more similar across conditions.

An alternative possibility is that the interaction of temporal codes is not based on representations of absolute duration, but rather relative duration. By this view, a transformation is applied to the temporal codes within each dimension that remaps the absolute durations onto a relative duration scale, one that lacks the granularity of metric representations. It has been argued that humans and other animals may use abstract, and shared 'magnitude' representations when dealing with spatial, temporal and numerical quantities (Walsh, 2003). This system necessarily lacks precise metric information for a particular dimension (e.g. that a stimulus lasted for 1083 ms, or subtended a visual angle of 87°), in order to provide a common coordinate space that allows for generalizations across dimensions (e.g. a 'high magnitude' code for stimuli which are 'long' or 'large'). While our experiments demonstrate a strong biasing effect from movement on perceived auditory duration, the interaction may occur at the level of these more abstract, relative codes, rather than reflect interactions of the absolute metrics. Indeed, an account based on the interaction of relative codes may also be considered consistent with the cross-experiment comparisons. The metrical difference between the two movement categories was much smaller in Experiment 3 and 4 (mean = 265.1 ms) compared to Experiments 1 and 2 (mean = 1376.5 ms), yet the biasing effect, while attenuated, remained relatively large (i.e., mean PSE difference of 53.6 ms in Experiments 3 and 4 compared to average of 128 ms in Experiments 1 and 2).

Given the present findings of integration of temporal codes across motor and sensory domains, the correlation between movement amplitude and movement duration may help to explain the emergence of common 'magnitude' representations in non-motor domains, where, for example, events that have larger spatial extent are judged to have longer duration (Casasanto & Boroditsky, 2008; Xuan, Zhang, He, & Chen, 2007; but see Rammsayer & Verner, 2014, 2015; Yates, Loetscher, & Nicholls, 2012). Movement duration cannot change without producing correlated changes in other physical dimensions of movement (e.g., speed as in Experiments 1 and 2, or space as in Experiment 3). These correspondences may lead to common magnitude representations even in sensory modalities where the dimensions are dissociable or, as in the present work, when the magnitude representations are associated with independent events.

In conclusion, the present four experiments provide evidence that sensory duration is biased towards concurrent motor duration. Our results place important constraints on theories used to model cue integration for state estimation, as well as models of time perception, action control and social cognition.

Author Note

Parts of the work reported here have been presented at scientific workshops. Abstracts from these workshops are accessible online, although none provide details about the experimental methods and results.

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