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Separable temporal metrics for time perception and anticipatory actions

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Reliable estimates of time are essential for initiating interceptive actions at the right moment. However, our sense of time is surprisingly fallible. For instance, time perception can be distorted by prolonged exposure (adaptation) to movement. Here, we make use of this to determine if time perception and anticipatory actions rely on the same or on different temporal metrics. Consistent with previous reports, we find that the apparent duration of movement is mitigated by adaptation to more rapid motion, but is unchanged by adaptation to slower movement. By contrast, we find symmetrical effects of motion-adaptation on the timing of anticipatory interceptive actions, which are paralleled by changes in perceived speed for the adapted direction of motion. Our data thus reveal that anticipatory actions and perceived duration rely on different temporal metrics.

Keywords: action; interception; perception; time perception

1. INTRODUCTION

Traditional models of human time estimation assume an internal clock that contains a temporal oscillator and a counter. Hypothetically, the counter accumulates neural pulses during the period to be estimated [1–3]. According to the traditional model there is just one internal clock, which is therefore involved in generating all temporal estimates, including those used for both time perception and motor planning [4,5]. However, the universality of timing mechanisms has recently been challenged.

After prolonged exposure (adaptation) to a moving stimulus, the apparent duration of a subsequent slower moving stimulus can seem mitigated [6–8]. This observation poses a fundamental challenge to the universality of human timing mechanisms, as the temporal distortions induced by motion-adaptation are spatially localized [8]. This encouraged us to question a common intuition that human time perception and the timing of anticipatory actions tap a common neural process, and therefore share a common temporal metric [9].

To assess whether anticipatory interceptive actions and time perception rely on a common or on different temporal metrics, we induced localized distortions of perceived duration via motion-adaptation. Consistent with previous reports, we find that motion-adaptation mitigates the perceived duration of subsequent slower movements, but has no impact on the perceived duration of more rapid movements [6–8]. These data contrast with the effects of motion-adaptation on the timing of anticipatory interceptive actions, which were both sped by adapting to slower movements, and slowed by adapting to more rapid movements. These changes in the timing of interceptive actions were paralleled by adaptation-induced changes in perceived speed for the adapted direction of motion. Our data thus reveal that the human central nervous system maintains multiple temporal metrics, as anticipatory

interceptive actions and time perception rely on separable estimates of time.

2. METHODS

Eight volunteers participated in this study. All had normal or corrected-to-normal visual acuity and gave informed consent prior to commencing the study, which was approved by the local Ethics Committee of the University of Queensland. All participants took part in experiments 1 and 4, whereas only seven took part in experiments 2 and 3.

Visual stimuli were generated using Cogent 2000 Graphics running in MATLAB 7.5 and were displayed on a 19 inch. Sony Trinitron G420 monitor at a resolution of 1280×1024 pixels and a refresh rate of 60 Hz. Participants viewed stimuli from 57 cm with their head placed in a chinrest. Responses were signalled via mouse button presses.

Adapting stimuli consisted of two circular rotating patterns (figure 1), each comprised six individual white dots with a luminance of 105 cd m^{-2} and a diameter subtending 0.88° of visual angle at the retina (dva). The dots moved against a dark background. The outer diameter of each pattern subtended 6.3 dva. Each pattern was centered 7.8 dva to the left and right of a central circular white fixation point (diameter = 0.5 dva). The pattern to the left of fixation rotated clockwise at an angular velocity of $68.5^\circ \text{ s}^{-1}$ (or 5.7g), while the pattern on the right rotated counter-clockwise at an angular speed of 821° s^{-1} (or 68.4g). Test stimuli consisted of presentations of a single dot with a luminance of 21.8 cd m^{-2} , matched in terms of its spatial properties to dots within adapting patterns.

(a) Experiment 1: speed judgement

As perceived duration can scale with apparent speed [10], we first quantified the impact of motion-adaptation on the perceived speed of our stimuli, so that we could later compensate for any changes when making duration judgements.

Each trial involved a sequential presentation of a standard and a comparison test stimulus, separated by a 500 ms inter-stimulus interval (figure 1a). Standard tests were offset to the

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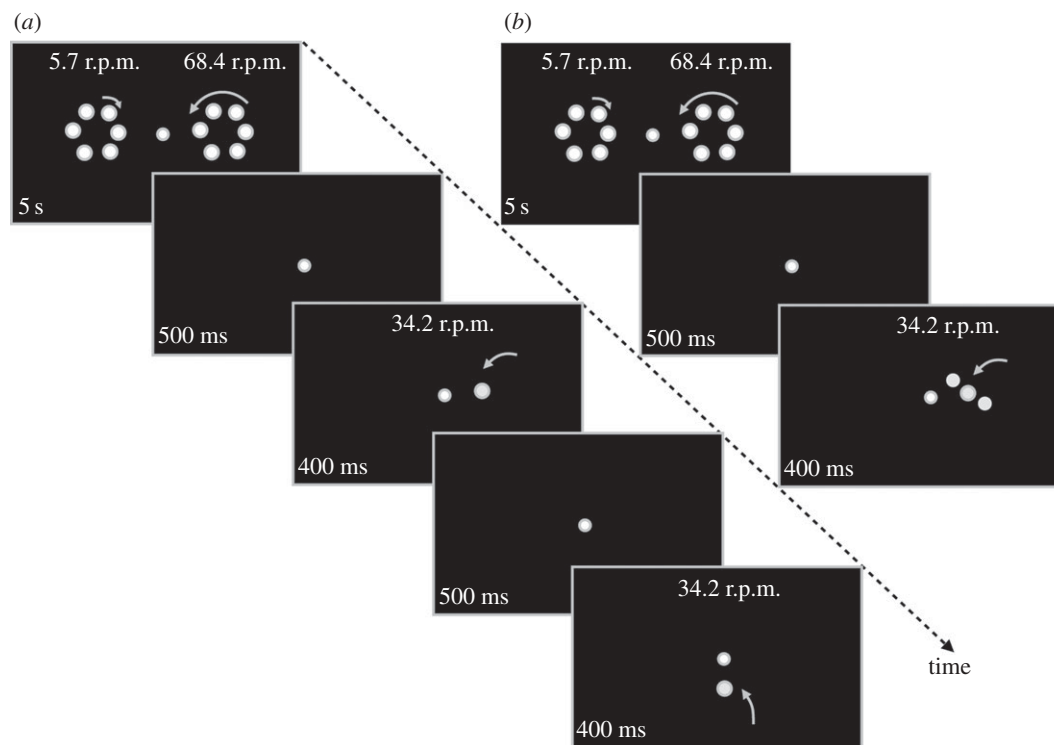


Figure 1. (a) Schematic of the time course of events during a trial in experiments 1 and 2. (b) Schematic of the time course of events during a trial in experiments 3 and 4. The two stationary circles served as a point of reference to judge the position of the moving test stimuli at onset and offset.

left or right of fixation (in an adapted location during adaptation runs of trials), whereas comparisons were offset an equal distance above or below fixation. Both the precise position of the comparison (above or below fixation) and the order of presentation (standard then comparison, or comparison then standard) were determined at random on a trial-by-trial basis. Test stimuli were presented for 300, 400 or 500 ms, determined at random on a presentation-by-presentation basis. This ensured that participants could not reliably judge apparent speed on the basis of distance travelled. Test trajectories were such that on average they passed the point closest to fixation at the mid-point of the test presentation (an angular position of 0° for tests above fixation, 90° for left tests, 180° for below tests and 270° for right tests). However, initial angular positions were jittered $\pm 45^\circ$ on a trial-by-trial basis to ensure that test speed was not reliably cued by starting or finishing positions. At the end of each trial, participants were asked to judge which of the two test stimuli had travelled fastest.

Test stimuli were viewed with (adaptation runs of trials) or without (baseline runs of trials) pre-exposure to adapting stimuli. During adaptation runs of trials, adapting stimuli were presented for 30 s on the first trial and for 5 s on subsequent trials. The speed of standard tests was constant (441° s^{-1} or 34.2 r.p.m.), whereas we manipulated comparison test speeds using a staircase method of adjustment. On the first presentation of each comparison, its speed was physically matched to the standard. Its speed was then adjusted in angular steps of 137° s^{-1} , up if the standard was said to be moving faster and down otherwise. Speed adjustments were reduced to angular steps of $34.2^\circ \text{ s}^{-1}$ after the second reversal in the pattern of response in each staircase (i.e. whereas on previous trials, the participant had reported that the standard had moved faster, they then reported that the comparison had moved faster, or vice versa).

There were four experimental conditions. Standard tests could be presented on the left and move in either the same or in a different direction relative to the adaptor, or standards could be presented on the right and move in the same or opposite direction as the adaptor. Standard and comparison tests rotated in the same direction in all trials. Presentations of each of the four conditions were interleaved. A run of trials finished after eight reversals within each of the four interleaved staircases. Each participant performed one run of baseline trials and one run of adaptation trials.

The speed at which comparisons seemed to match standards was estimated by averaging comparison speeds across the final five reversal points in each staircase. The effects of adaptation were then given by the difference between these matched speed estimates during adaptation runs of trials and baseline runs of trials, with a positive value signifying that the adapted stimulus seemed to be moving *slower* after adaptation.

(b) Results

As can be seen in figure 2a, robust adaptation-induced speed changes were observed in all experimental conditions. Adaptation to a relatively slow-moving stimulus *increased* the perceived speed of tests in the adapted location that rotated in the same direction as the adaptor ($t_7 = 3.87$, $p = 0.006$, $r = 0.82$) but *reduced* the perceived speed of tests rotating in the opposite direction ($t_7 = 3.55$, $p = 0.009$, $r = 0.80$). By contrast, adaptation to relatively fast motion reduced the perceived speed of tests in the adapted location *regardless* of the direction of rotation (same direction: $t_7 = 3.75$, $p = 0.007$, $r = 0.81$; opposite direction: $t_7 = 3.86$, $p = 0.006$, $r = 0.82$).

(c) Experiments 2a and 2b: perceived duration

Having quantified the impact of motion-adaptation on perceived speed, we then measured the impact of motion-adaptation

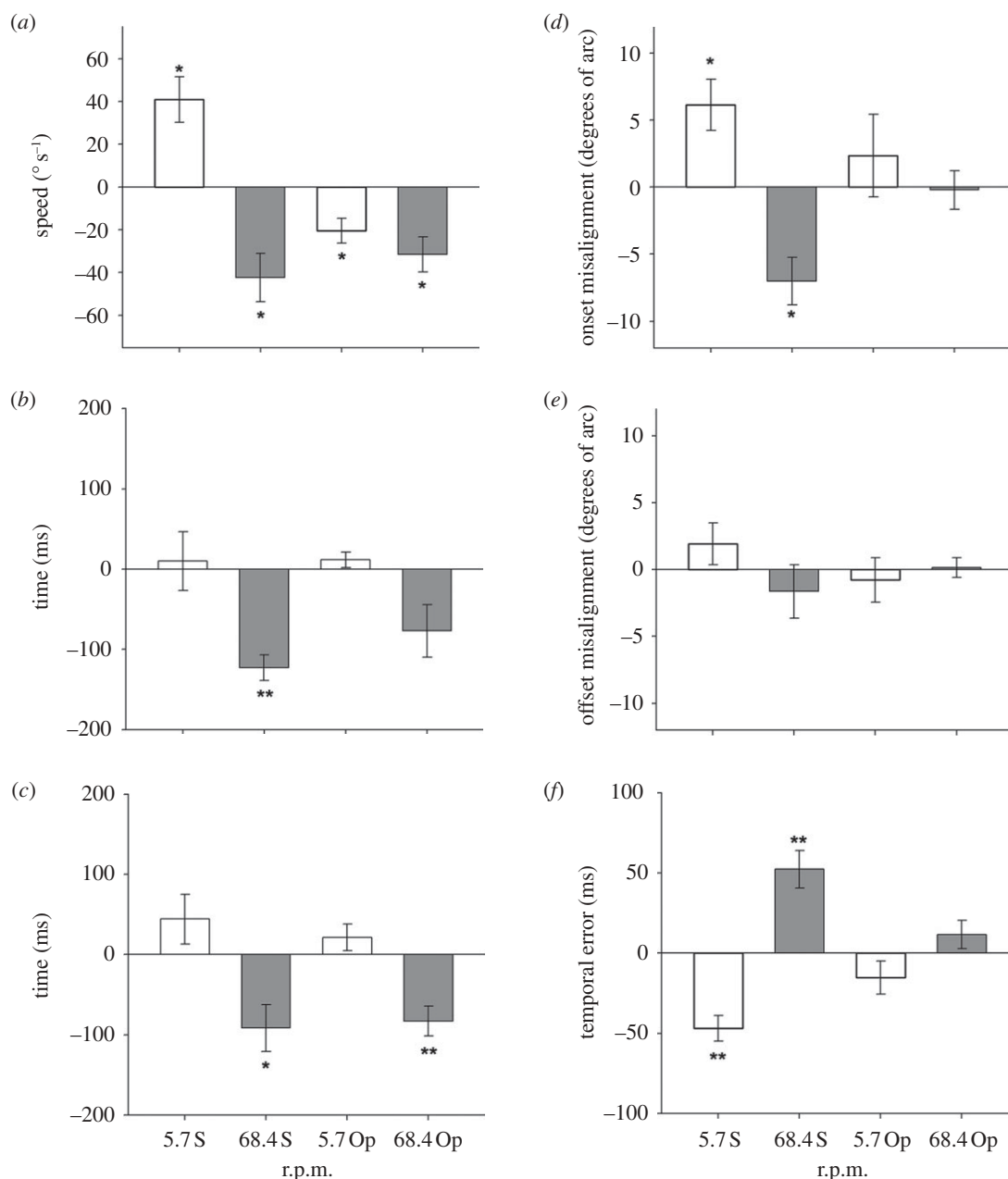


Figure 2. (a) Changes in perceived speed after motion-adaptation. Positive values show that perceived speed increased relative to baseline, whereas negative values signify reductions in perceived speed (experiment 1). Motion-adaptation-induced changes in perceived duration relative to unadapted comparisons matched in terms of physical speed (b, experiment 2a) or perceptual speed (c, experiment 2b). Motion-adaptation-induced misalignment between moving tests and static reference points at onset (d, experiment 3a) and offset (e, experiment 3a). Measurements are in angular degrees of arc. (f) Temporal errors to synchronize the arrival of the moving test stimulus at the position of the two stationary markers (experiment 4). S, test stimulus moved in the same direction as the adaptor; Op, test stimulus moved in the opposite direction as the adaptor; r.p.m., rotations per minute. * $p < 0.05$, ** $p < 0.01$. Error bars show ± 1 s.e.m.

on perceived duration. Details concerning experiments 2a and 2b were as for experiment 1, with the following exceptions.

In experiment 2a, comparison test speeds were fixed and physically matched to standards. In experiment 2b, during adaptation runs of trials, comparison speeds were set according to the results of experiment 1 to match the perceived speeds of standard tests. In both experiments, the durations for which comparisons were presented were manipulated according to a staircase procedure. On the first trial of each staircase, comparisons and standards were matched in terms of duration (400 ms). Comparisons were then adjusted in steps of 100 ms, reduced to steps of 50 ms in each staircase after two reversals. The comparison duration seemingly

matched to the standard was estimated by averaging comparison durations across the final five reversal points in each staircase. The effects of adaptation were then given by the difference between matched duration estimates from baseline and adaptation runs of trials, with a negative value signifying the adapted stimulus seemed to have a *shortened* duration after adaptation.

(d) Results

As can be seen in figure 2b, adaptation to a slow-moving stimulus did not change the perceived duration of test stimuli in adapted locations. This was true regardless of whether tests rotated in the same direction as the adaptor ($t_6 = 0.27$,

$p = 0.79$, $r = 0.10$) or in the opposite direction ($t_6 = 1.18$, $p = 0.27$, $r = 0.43$). Adapting to faster movement, however, caused a reduction in the perceived duration of tests in adapted locations that moved in both the same ($t_6 = 7.82$, $p < 0.001$, $r = 0.95$) or opposite ($t_6 = 2.36$, $p = 0.055$, $r = 0.69$) directions as the adaptor, although this last effect was less robust for opposite direction tests.

While physically matched in experiment 2a, owing to motion-adaptation, the perceived speeds of standard and comparison tests differed. To ensure this was not responsible for apparent duration distortions, we repeated the experiment using comparisons adjusted to match perceived standard speeds. As can be seen in [figure 2c](#), results were qualitatively similar to those of experiment 2a. Adaptation to slower movement did not distort the perceived duration of tests in the adapted location (same direction as adaptation $t_6 = 1.43$, $p = 0.20$, $r = 0.50$; opposite direction $t_6 = 1.30$, $p = 0.23$, $r = 0.46$). Adaptation to faster movement, however, reduced the perceived duration of tests in adapted locations (same direction as adaptation $t_6 = 3.13$, $p = 0.02$, $r = 0.78$; opposite direction $t_6 = 4.42$, $p = 0.004$, $r = 0.87$).

(e) *Experiments 3a and 3b: motion-adaptation and perceived positions at onset and offset*

In experiments 2a and 2b, we demonstrated that adaptation to relatively fast movement can reduce the apparent duration of a moving dot in an adapted location relative to a corresponding dot in an unadapted location. This was true regardless of whether the speed of the dots was matched physically (experiment 2a) or perceptually (experiment 2b). This ensured that the duration of distortions of experiment 1 could not be attributed to differential physical or perceived speeds.

When judging a physically moving stimulus, one could extract an implicit estimate of duration by judging the distance travelled. To ensure that the apparent duration distortion we have observed cannot be attributed to a distortion in apparent distance travelled, we measured the impact of motion-adaptation on the apparent location of moving stimuli at onset (experiment 3a) and offset (experiment 3b).

Experimental details for experiments 3a and 3b were as for experiment 1, with the following exceptions. In a *t*-test a pair of static reference dots (luminance and size-matched to test stimuli) were positioned abreast (offset 0.7 dva) of the average starting (experiment 3a) or finishing (experiment 3b) location of the test dot ([figure 1b](#)). The precise position of this reference was manipulated on a trial-by-trial basis using a staircase method of adjustment. On average, the starting (experiment 3a) and finishing (experiment 3b) position of the test was at the point of the rotation cycle nearest fixation (a Cartesian angular position of 90° for left tests, and 270° for right tests). However, the precise starting/finishing position, along with that of the reference, was jittered $\pm 45^\circ$ on a trial-by-trial basis to ensure that the position of the reference did not reliably cue the onset/offset location. At the end of each trial, participants were asked to judge if the test onset or offset location was advanced or lagging relative to the reference. Trials were completed with (adaptation runs of trials) or without (non-adaptation) pre-exposure to the adapting stimulus.

(f) *Results*

The results of experiment 3a are depicted in [figure 2d](#). These data reveal that the perceived onset location of moving tests was modulated by same direction adaptation. Adapting to

slower movement resulted in tests seeming to onset in advanced positions relative to baseline ($t_6 = 3.20$, $p = 0.018$, $r = 0.79$), whereas adapting to faster movement resulted in tests seeming to appear at retarded locations ($t_6 = 3.94$, $p = 0.007$, $r = 0.85$). By contrast, perceived onset locations were not modulated by opposite direction adaptation (slow adaptor: $t_6 = 0.76$, $p = 0.47$, $r = 0.29$; fast adaptor: $t_6 = 0.15$, $p = 0.88$, $r = 0.06$).

The results of experiment 3b are depicted in [figure 2e](#). These data reveal that the perceived offset locations of moving tests were neither impacted by motion-adaptation when moving in the same direction as the adaptor (slow adaptor: $t_6 = 1.23$, $p = 0.26$, $r = 0.44$; fast adaptor: $t_6 = 0.82$, $p = 0.44$, $r = 0.31$) or when moving in the opposite direction as the adaptor (slow adaptor: $t_6 = 0.47$, $p = 0.65$, $r = 0.18$; fast adaptor: $t_6 = 0.18$, $p = 0.85$, $r = 0.07$).

Distance travelled can provide an implicit measure of the duration of a moving stimulus. In experiment 3a, apparent test onset locations were advanced via adaptation to slower same direction motion and retarded by adaptation to faster same direction movement. Given that adaptation did not impact on apparent test offset locations, we can estimate apparent duration distortions entirely on the basis of the distortion in apparent onset location. This should have resulted in adaptation to faster movement bringing about an *increase* in perceived duration, as this adaptation led to tests seeming to onset at retarded positions, and therefore to travel a greater distance relative to baseline. However, we know from experiment 2 that adaptation to faster movements resulted in the opposite effect, a mitigation of perceived duration. This discredits any explanation of the adaptation-induced duration distortion resulting from a distortion in apparent distance travelled. Moreover, adapting to slower movement also distorted apparent onset location, but this type of adaptation had no impact on perceived duration, further discrediting a link between these two distortions.

(g) *Experiment 4: motion-adaptation and anticipatory interceptive timing*

In experiment 4, we sought to determine whether motion-adaptation would impact anticipatory interceptive actions. More specifically, we were interested to see if anticipatory interceptive timing would reflect the temporal metric that underlies duration perception.

Details concerning experiment 4 were as for experiment 3b with the following exceptions. On each trial, participants were asked to press a button to mark the time that a moving test dot became aligned with a pair of static reference markers. The duration of the test stimulus was 800 ms, with the test becoming aligned with the reference markers after 600 ms. Test movement then persisted for 200 ms before it disappeared. During a run of trials, participants performed 12 trials for each of the four experimental conditions—48 trials in total. Participants completed one baseline and one adaptation run of trials.

(h) *Results*

The results of experiment 4 are depicted in [figure 2f](#). These data show that motion-adaptation can have an impact on the timing of anticipatory interceptive actions. Adapting to relatively slow movement in the same direction as the test, which causes an illusory increase in perceived test speed (see experiment 1), resulted in participants pressing a button *earlier* to mark the point in time that the moving test had become

aligned with the static reference ($t_7 = 5.84$, $p < 0.001$, $r = 0.91$). Adapting to relatively fast same direction movement, which causes an illusory decrease in apparent test speed, resulted in later button presses ($t_7 = 4.49$, $p = 0.003$, $r = 0.86$). By contrast, adapting to opposite directional motion did not have an impact on the timing of anticipatory interceptive actions (slow adaptor: $t_7 = 1.47$, $p = 0.18$, $r = 0.48$; fast adaptor: $t_7 = 1.29$, $p = 0.23$, $r = 0.43$).

A repeated-measures ANOVA contrasting these results and those obtained in experiment 2b revealed a significant two-way interaction between experiment and adaptor speed ($F_{1,6} = 31.10$, $p < 0.001$, $r = 0.91$). There was also a significant three-way interaction involving experiment, adaptor speed and test stimulus direction ($F_{1,6} = 7.88$, $p = 0.031$, $r = 0.75$). These data establish that adaptor speed and test direction had differing effects on judgements of perceived duration (experiment 2b) and on the timing of interceptive actions (experiment 4). Specifically, as can be seen by contrasting figures 2c and f, whereas adaptation to relatively slow movement had no impact on the perceived duration of tests (experiment 2b), it sped anticipatory actions (experiment 4), but only if tests moved in the same direction as the adaptor.

3. GENERAL DISCUSSION

The main goal of the experiments reported here was to determine if perceptual estimates of the passage of time involve the same metric as estimates of time-to-arrival for anticipatory interceptive actions. To examine this question, we adapted to movement, thereby creating a localized distortion in the apparent duration of subsequent motion [6–8]. Critically, consistent with previous studies, adapting to relatively fast movement mitigated the apparent duration of subsequent motions, but adapting to relatively slow motion caused no such distortion [6–8]. Here, we have shown that motion-adaptation has a qualitatively different impact on anticipatory interceptive actions, which were both hastened by adapting to relatively slow motion, but also delayed by adapting to faster movement.

Our data suggest that duration perception is not determined by the mechanism responsible for time-to-arrival estimates during interceptive actions. This implies that not only do we have modality specific internal clocks [11–13] that are spatially localized [8,11,14], but that we also employ different clocks when implementing different behavioural goals, even when achieving those goals depends on the same sensory input.

The results of experiments 3a and 3b indicate that the impact of motion-adaptation on perceived duration cannot be attributed to changes in the apparent distance traversed by a moving test. If anything, these results suggest the opposite distortion to that which ensues. Adaptation had no discernible impact on the test stimulus offset location, but systematically modulated the apparent position of the test at onset. Adapting to relatively fast movement caused the test stimulus to be seen at retarded locations (at an earlier point within its physical trajectory), whereas adapting to slower movement caused the test to be seen in more advanced positions. Thus, the apparent distance traversed, after fast motion-adaptation, would tend to be exaggerated, which would take longer assuming a fixed speed. However, such adaptation results in a mitigation of perceived duration. Although this was

not the primary emphasis of the paper, to the best of our knowledge, these data constitute the first evidence that the apparent position of a moving stimulus at onset can be modulated via motion-adaptation.

Our data suggest that, to some extent, temporal estimates of time-of-arrival for interceptive actions might reflect perceived speed [15,16]. This link is suggested by the fact that adapting to relatively slow same direction movement resulted in tests seeming to move faster (figure 2a) and in anticipatory interceptive actions being implemented earlier (figure 2f). Similarly, adapting to relatively fast same direction movement resulted in tests seeming to move more slowly and in anticipatory interceptive actions being implemented later. However, there is a dissociation. Adapting to opposite direction movement resulted in tests seeming to move more slowly (figure 2a) but had no discernible impact on the timing of anticipatory interceptive actions (figure 2f). Recently, it has been suggested that perceived speed relies on a combination of direction-tuned mechanisms and non-directional temporal frequency filters [17]. Our data suggest that the timing of anticipatory interceptive actions solely reflects the activity of direction-tuned mechanisms, thereby allowing for a dissociation between perceived speed and anticipatory action timing when adapting to opposite direction movement.

Results concerning the impact of motion-adaptation on perceived duration suggest the opposite contingency relative to anticipatory interceptive actions. While direction of motion was critical for anticipatory interceptions, it was irrelevant for adaptation-induced distortions of perceived duration. Also, duration perception was only distorted by adapting to relatively fast movement. Previously, this last observation has prompted the proposal that perceived duration distortions might be tied to adaptation at early stages of the magnocellular pathway [6–8,18], where cells are primarily responsive to high temporal frequencies and are insensitive to the direction of motion [19]. Our data are consistent with this proposal.

One clear difference between two of the temporal tasks employed here—duration judgements and anticipatory interceptive actions—concerns the nature of the knowledge required to accomplish them. In duration judgements, participants are obliged to demonstrate explicit post hoc knowledge about the time intervals of interest, whereas anticipatory actions involve implicit knowledge, a predictive temporal judgement reflecting time-to-arrival and therefore the time remaining until an action is required [20]. It remains to be seen if this distinction, between explicit and implicit knowledge of time, is responsible for the dissociation between time perception and interceptive action timing that we have discovered.

4. SUMMARY

We have demonstrated that there are qualitative differences between the impact of motion-adaptation on perceived time and on the timing of anticipatory interceptive actions. Time perception is mitigated by adapting to relatively fast movement, but is unaffected by adapting to slower motion. This contrasts with the timing of interceptive actions, which are slowed by adapting to relatively fast motion and sped by adapting to slow movement. These data reveal that time perception and time-to-arrival estimates during interceptive actions rely on different temporal

metrics, and that we employ distinct timing mechanisms when implementing different behavioural goals.

This study was approved by the local Ethics Committee of the University of Queensland.

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