Time-dilation and time-contraction in an anisochronous and anisometric visual scenery

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Several studies show that visual stimuli traveling at higher velocities are overestimated with respect to slower, or stationary, stimuli of equivalent physical duration. This effect—*time dilation*—relates more in general to several accounts highlighting a quantitative relationship between the amount of changes a stimulus is subject to and the perceived duration: faster stimuli, subject to a greater number of changes in space, lead to overestimated durations of displacement. In the present paper we provide evidence of a new illusory effect, in which the apparent duration of a sensory event is affected by the way a constant number of changes are delivered in time, or in time and space. Participants judged accelerating and decelerating sequences of stationary flickering stimuli (Experiments 1 and 3) and accelerating and decelerating horizontally drifting visual stimuli (Experiment 2) on the fronto-parallel plane. Acceleration and deceleration were achieved by irregular sequencing of events in time (anisochronous flicker rate) or irregular sequencing of events in time and space (anisochronous and/or anisometric drift). Despite being characterized by the same amounts of visual changes, accelerating and decelerating sequences lead to opposite duration biases (underestimation and overestimation errors, respectively). We refer to this effect in terms of ATI: Aniso-Time-Illusion. This bias was observed in both subsecond (760 ms) and suprasecond ranges (1900 ms). These data highlight how the spatio-temporal evolution of dynamic visual events, asides the overall quantity of changes they are subject to, affect the perceived amount of time they require to unfold.

Keywords: time-dilation, time perception, temporal frequency, stimulus motion, acceleration

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Introduction

Temporal information frames a great portion of our daily experience. Playing a musical instrument at the correct tempo, articulating our speech, and moving and reacting to predicted events are all possible given our ability of appropriately coding and implementing specific target durations. Several studies show that our sense of time can be distorted via a variety of manipulations, which highlight how perceived durations are subject to highly constructive processes. Time is an interpretation our nervous system performs to provide a structure for changes occurring in our environment or subtending our behaviors. Timing estimates are known, for example, to be affected by a variety of nontemporal factors such as numerosity, size, luminance (Xuan, Zhang, He, & Chen, 2007), predictability (Pariyadath & Eagleman, 2007; Ranganath & Rainer, 2003; Tse, Intriligator, Rivest, & Cavanagh, 2004; Ulrich, Nitschke, & Rammsayer, 2006), and familiarity (Witherspoon & Allan, 1985).

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An important set of examples is provided by several experimental accounts demonstrating how displacement information affects timing computations. These studies show that timing estimates of moving stimuli are proportional in size to stimulus velocity (Brown, 1995; Goldstone & Lhamon, 1974; Kanai, Paffen, Hogendoorn, & Verstraten, 2006; Roelofs & Zeeman, 1951). Faster stimuli are overestimated with respect to slower and stationary stimuli (*time dilation*). A subset of these studies reveal two important pieces of information: (a) Timing biases are best explained by a *change-based* account of timekeeping performance (i.e., subjective passage of time is indexed by the number of physical changes occurring within an objective time frame) and (b) Motion—a continuous change of space—acts as an important stimulus duration cue (Kanai et al., 2006). Kanai et al. (2006) attempted to isolate the source of this effect by dissecting visual motion into its physical constituents: motion trajectory and coherence, spatial frequency, temporal frequency, and velocity, given by the ratio of these two latter variables. Throughout a series of experiments, the authors established that the critical factor subtending the illusion was represented by temporal frequency (hertz, or rate of change in time), as the time dilation effect could be even observed in a stationary flickering Gaussian blob. A similar study was also recently conducted by Kaneko & Murakami (2009) using slightly different stimulus configurations (horizontally drifting Gabor-patch stimuli vs. concentric expanding gratings used by Kanai et al.) to address the quantitative relationship between stimulus motion and stimulus apparent duration. These latter authors observed that stimulus velocity (temporal frequency/spatial frequency ratio) provided the best estimator of stimulus duration overestimations. This led the authors to determine the visual processing pathway area MT as the most likely neuroanatomical candidate for the time dilation effect, since it hosts neuronal subpopulations selectively tuned to stimulus speed (Kaneko & Murakami, 2009; Perrone & Thiele, 2001; Priebe, Lisberger, & Movshon, 2006). Despite these slightly different conclusions, presumably due to the adoption of different stimulus configurations (Kaneko & Murakami, 2009), both studies frame results in accordance to a change-based interpretation of time indexing. Time dilation relates more in general to the *filled-duration illusion*, in which the number of changes delimiting a period of stimulation affects its overall perceived duration.

Time-dilation studies provide clear indications of how subjects exploit regular and constant rates of change in time and/or space to produce estimates of elapsed duration. Regular dynamics, however, only represent a portion of the spectrum of changes that commonly take place in our environment. The core motivation of the present study was therefore that of assessing how variable dynamics, as those that characterize accelerating and decelerating motion, affect our estimation of durations. We did so by using ecologically significant accelerating and decelerating configurations obtained by sequencing in opposite ways the same number of visual events. This approach enables us to pose a slightly different question within the time-dilation literature; instead of focusing on the effects of higher or lower rates of change, we can obtain insights into how equal amounts of change, which evolve differently in time, affect our time percepts.

In the first experiment, participants performed estimation of stationary flickering stimuli characterized by anisochronous (progressive change in temporal domain—hertz) sequential patterns of presentation. This was tested for both subsecond and suprasecond duration ranges. Participants also estimated partially randomized flicker sequences in the attempt of isolating primacy/recency factors driving response biases. In a second experiment subjects evaluated the duration of drifting Gabor patch stimuli which appeared to either accelerate or decelerate by means of anisochronous (progressive change in temporal domain—hertz) and/or anisometric (progressive change in spatial domain—degrees of phase shift per draw cycle) dynamics, in order to extend the manipulation to horizontal spatial displacement. Finally, in a third experiment, we replicated Experiment 1 using stimuli which were set at isoluminant levels with the background, thus enabling to test whether the illusion was dependent on luminance based contrast.

EXPERIMENT 1a: effects of anisochronous sequencing on the estimated duration of suprasecond stationary flickering visual stimuli

Methods

Participants

Eight volunteers with normal or corrected to normal vision participated in the first experiment (four male; mean age = 27.3, +/− 3.3 years). All participants gave informed consent and were debriefed on the goals of the experiment once concluded.

Stimuli and task conditions

Within a classical forced choice psychophysical paradigm, participants compared an isochronous standard intermittent sequence of visual stimuli (nine

successive 50-ms circular stimuli interleaved by eight 181-ms pauses; total duration was 1898 ms) to a control isochronous or anisochronous probe sequence (nine 50-ms flashes interleaved by a sequence of constant 181-ms pauses or progressively longer or shorter pauses *decelerating*: pause(i) = $(200 + i^3)/2$ vs. *accelerating*: pause(i) = $[200 + (9 - i)^3]/2$; i = 1 through 8; total duration = 1898 +/− Δt; see Figure 1). Given that the probe pause durations were calculated according to a cubic function, this means we are technically dealing with jerk (i.e., the derived function of acceleration, change of acceleration over time) and not acceleration, which would correspond to a quadratic function. Nevertheless, for sake of simplicity we refer to this manipulation simply in terms of acceleration/deceleration; from a visual standpoint people have an intuitive sense of what acceleration *looks like*, while the same cannot be said for jerk. The change in t (Δt) was added or subtracted to the eight pause durations of the probe sequences (isochronous control and anisochronous). For example, if within a trial a value of Δt = −600 was selected, then 75 ms (−600/8) would be subtracted from each pause. The standard sequence never varied in duration.

Each circular stimulus encompassed approximately 4° of visual angle at a 57-cm viewing distance; the first and the last circular stimuli in each sequence were red (Stimulus 1 and Stimulus 9 in Figure 1), while the seven intermediary stimuli were black. This was done so subjects had a clear idea when each sequence terminated, thus preventing them from anticipating further stimuli. All stimuli appeared over a grey background. Within each trial, the type of probe sequence (isochronous vs. accelerating vs. decelerating) and the value of Δt (−600, −400, −200, 0, 200, 400, 600) were randomly selected. Each subject performed 40 repetitions for probe type (3 sequence types × 7 Δt values), for a total

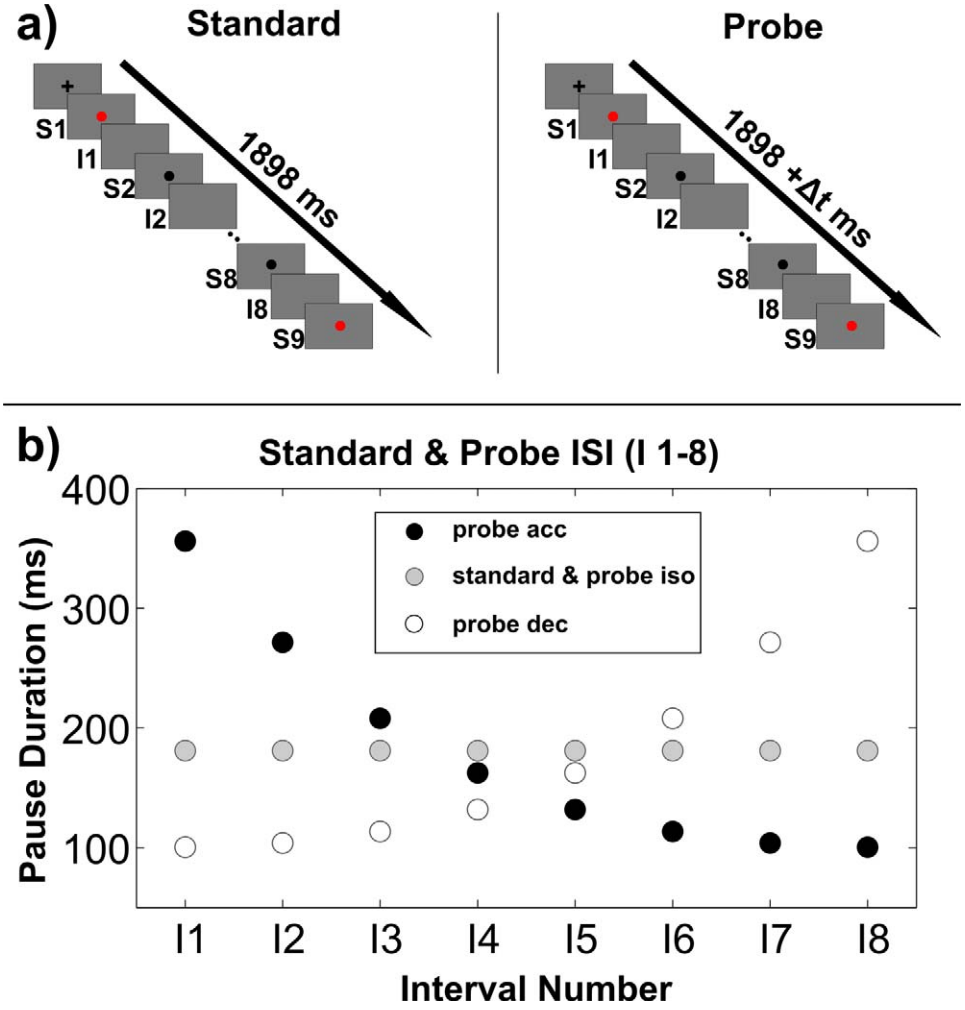

Figure 1. (a) Experiment 1 standard and probe stimulus sequences = 9 stimuli + 8 inter stimulus intervals (ISI) each. Each stimulus (1–9) lasted 50 ms in both the standard and probe sequences. The standard sequence had a constant duration of 1898 ms, while the probe duration could vary between 1298 ms and 2498 ms. (b) Stimulus sequence ISI durations (Intervals 1–8). In the standard sequences the ISIs were isochronous (ISO), while in the Probe condition the ISIs were progressively shorter—accelerating (ACC), progressively longer—decelerating (DEC), or control-isochronous (ISO).

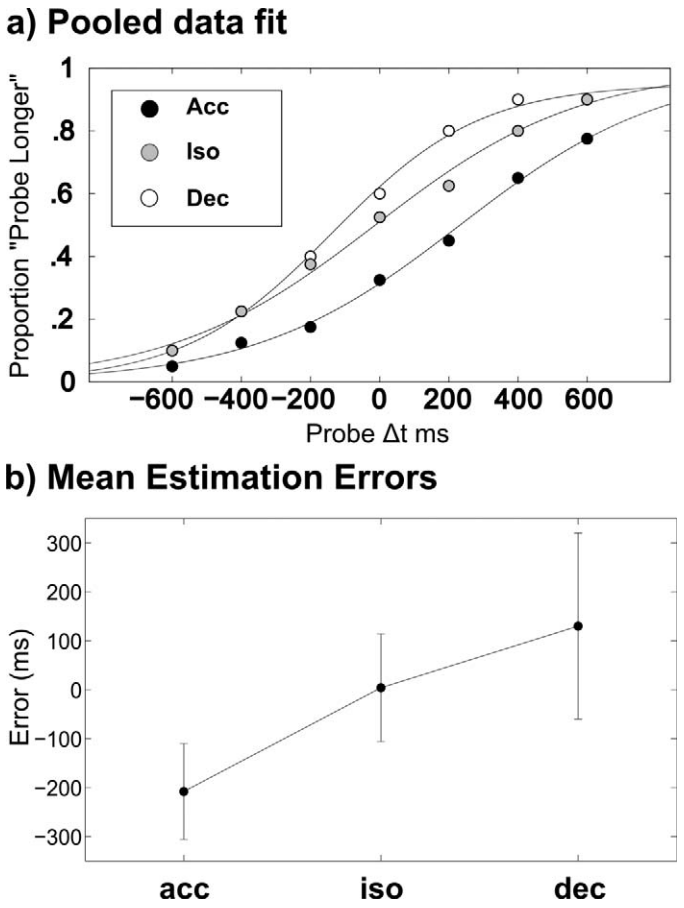

Figure 2. (a) Experiment 1a pooled subject data logistic fit for accelerating, decelerating, and isochronous probes. (b) Mean Estimation errors (positive values = overestimation; negative values = underestimation; error corresponds to the point of subjective equality with opposite sign; i.e., error = -PSE) for accelerating, decelerating, and isochronous probes.

of 840 trials. Participants were informed not to attend the number of stimuli within each sequence as their numerosity (constant) would not be informative of the sequence's duration. Also, participants were instructed to not "count seconds" or aid their performance with subvocalization strategies.

Within this setup, for $\Delta t = 0$, we have an equal average temporal frequency (i.e., average flicker rate) for both the standard and the probe animations; biased accounts will therefore be exclusively determined by sequential stimulus placement and not by overall amount of samples presented within the 1898-ms time window. Each trial began with the presentation of a central fixation cross and an acoustic cue. Participants were instructed to maintain fixation until the end of the trial; head movements were restrained by a chinrest and viewing distance was kept at 57 cm. After a 750-ms delay, the first sequence (standard or probe, counterbalanced across participants) was presented, and this was followed by a 1500-ms pause by the second sequence (probe or standard). Standard/probe sequence order was counterbalanced to avoid recency or primacy potential confounds across sequences. At the end of each trial participants were instructed to indicate by pressing a mouse button whether the second sequence was longer or shorter than the first one. The coding of mouse responses was counterbalanced within participants. The next trial began 750 ms after the emitted response. Stimuli delivery and response collection were implemented on E-prime v1.1. Stimuli were presented on a 15" IBM G-52 cathode ray tube monitor with 60 Hz refresh rate.

Analysis

Single subject and pooled subject data were fitted with a logistic psychometric function. The resulting values of parameters alpha (PSE: value of Δ-t required for the duration of the probe sequence to appear identical to that of the standard sequence) and beta of the psychometric function (sensitivity to change in Δ-t) were compared across control isochronous and accelerating/decelerating anisochronous sequences, in order to identify shifts in PSE and/or variations in sensitivity consequent to stimulus temporal sequencing.

Analyses were carried out on MATLAB 7.0 (The MathWorks, Inc.) and STATISTICA 7 (StatSoft, Inc.). Psychometric functions were fitted using the *psignifit* toolbox for MATLAB, version 2.5.6 (www.bootstrap-software.org), which implements the maximum-likelihood method (Wichmann & Hill, 2001a, 2001b).

Results

A pooled data logistic fit revealed opposite effects of accelerating and decelerating probe sequences on timing estimates (for $\Delta t = 0$, accelerating PSE = 232 ms underestimation vs. decelerating PSE = 115 ms overestimation, while control isochronous probes show no estimation bias; Figure 2a).

A 3 × 2 factorial ANOVA (Probe Sequence: *accelerating* vs. *isochronous control* vs. *decelerating* × Stimulus Order: *standard-probe* vs. *probe-standard*) performed on participant's alpha values (PSE) revealed a significant main effect of Probe Sequence [$F(2, 12) = 10.123$, $p < 0.01$], no effect of Stimulus Order [$F(1, 6) = 0.15$, p n.s.], and no significant Probe Sequence × Stimulus Order interaction [$F(2, 12) = 1.09$, p n.s.] (Figure 2b). A Fisher LSD post-hoc analysis conducted on Probe Sequence revealed that an accelerating probe significantly differed from both an isochronous and a decelerating probe ($p < .05$ and $p < 0.01$, respectively), while a decelerating probe did not significantly differ from an isochronous probe. Thus, when related to the

isochronous control sequence, accelerating and decelerating probes did not yield completely symmetrical effects. In absolute terms, accelerating sequences resulted in greater biases than decelerating sequences (underestimations and overestimations, respectively). The lack of a Stimulus Order main effect and Probe Sequence × Stimulus Order interaction ruled out the presence of primacy or recency effects related to order of standard and probe delivery.

An equivalent 3 × 2 factorial ANOVA was performed on participants' beta parameter values. No effects of Probe Sequence [$F(2, 12) = 1.887$, p n.s.], Stimulus Order [$F(1, 6) = .235$, p n.s.], and no Probe Sequence × Stimulus Order interaction [$F(2, 12) = 1.457$, p n.s.] were recorded. Therefore, Probe Sequence and Stimulus Order had no impact on participant's sensitivity to change in Δt: task difficulty (the ability of performing a standard–probe duration discrimination at different values of Δt) was not modulated by either of these variables.

Discussion

The core finding of the first experiment was that accelerating and decelerating patterns of flickering stationary visual stimuli were underestimated and overestimated respectively with respect to control isochronous sequences of equivalent physical duration, despite providing an equal amount of samples across the sequence time window. This represents a novel finding within the time dilation effect literature as opposite perceptual effects can be determined by the manipulation of stimulus dynamics independently of the amount of information delivered within a physical time window. A stationary isochronous sequence was shown by Kanai et al. (2006) to evoke equivalent duration estimations to those of a physically displaced visual stimulus; thus, it is presumable that anisochronous sequences equivalently triggered some form of motion processing in which subjects interpreted these flashes as accelerating or decelerating moving objects and applied a heuristic in the line of accelerating equals covering ground in less time whereas decelerating equals covering ground in more time (this is further explored in Experiment 2).

Several studies distinguish between time perception in the subsecond and suprasecond ranges (Buonomano, Bramen, & Khodadadifar, 2009; Näätänen, Syssoeva, & Takegata, 2004; Rammsayer, 1999; Rammsayer & Lima, 1991). Subsecond intervals seem to elicit an automatic/sensory form of timing, while longer suprasecond intervals elicit cognitively assisted forms of timing. In the following experiment we wanted to ascertain whether the illusion could be reproduced in the subsecond interval range.

EXPERIMENT 1b: effects of anisochronous sequencing on the estimated duration of subsecond stationary flickering visual stimuli

Methods

Participants

Eight volunteers with normal or corrected to normal vision participated in the experiment (four male; mean age = 29.7, +/− 2.9 years). All participants gave informed consent and were debriefed on the goals of the experiment once concluded.

Stimuli and task conditions

Participants estimated subsecond anisochronous flickering stimuli in a similar task to that of Experiment 1a. Standard and probe sequences were constructed by downscaling both the duration of each circular stimulus and the duration of pauses separating consecutive stimuli by a factor of 2.5. These sequences were therefore identical to those of Experiment 1a except for their overall duration. In this experiment, subjects compared within each trial an isochronous standard sequence (760 ms) to an accelerating or decelerating anisochronous probe. In half the trials standard and probe sequences shared the same duration, while in the other half of trials the probe could last 150 ms longer (910 ms) or 150 ms shorter (610 ms) than the standard. Subjects performed a total of 160 trials (80 trials with probe $\Delta t = 0$, 40 trials with $\Delta t = 150$, and 40 trials with $\Delta t = -150$). As in Experiment 1a, subjects indicated at the end of each trial whether the second sequence lasted longer or shorter than the first sequence. Sequence order was counterbalanced across participants.

Analysis

Since our goal was simply that of establishing if the effects uncovered in Experiment 1a could be replicated for subsecond intervals, we only analyzed the proportion of "probe longer" responses for probe sequences with $\Delta t = 0$ (40 accelerating and 40 decelerating probes), while the remaining probe sequences were treated as flankers and were excluded from the analysis.

Results

Responses for probe sequences with $\Delta t = 0$ were entered into a 2 × 2 factorial ANOVA (Probe Sequence: *accelerating* vs. *decelerating* × Stimulus

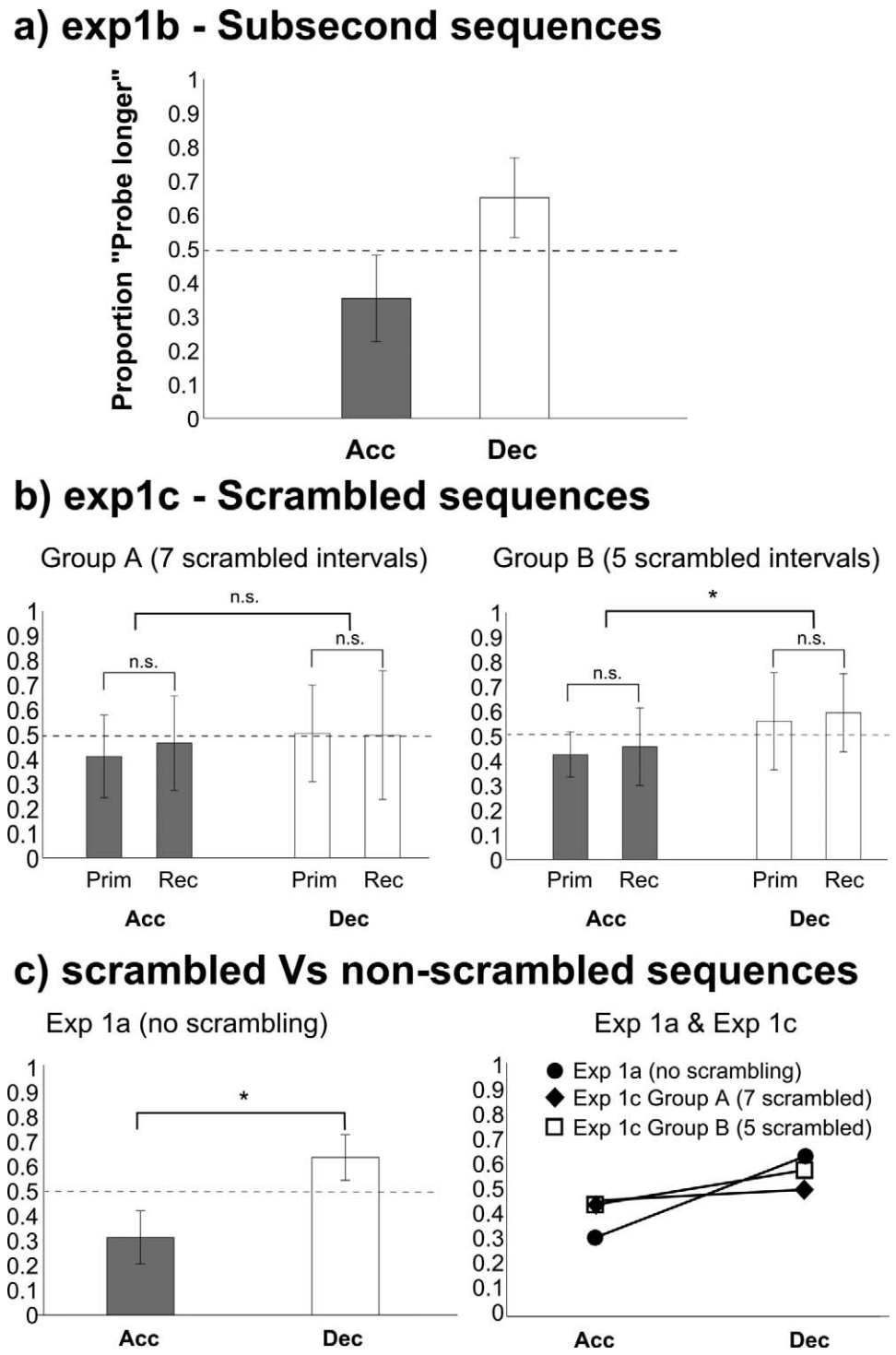

Figure 3. (a) Proportion of "probe longer" responses for subsecond accelerating and decelerating probe sequences of equal duration to the standard sequence ($\Delta t = 0$ ms). (b) Proportion of "probe longer" responses for Group A and Group B scrambled probe sequences with $\Delta t = 0$ ms. (c) Comparison of Experiment 1a (nonscrambled) and Experiment 1c (scrambled) responses for probe sequences with $\Delta t = 0$ ms.

Order: *standard-probe* vs. *probe-standard*). The analysis revealed a significant effect of Probe Sequence [$F(1, 6) = 19.81$, $p < .01$], no effect of Stimulus Order [$F(1, 6) = 5.23$, p n.s.], and no Probe Sequence × Stimulus Order interaction [$F(1, 6) = .05$, p n.s.]. Analogous to Experiment 1a, accelerating sequences produced time contraction while decelerating sequences resulted in time expansion (Figure 3a).

Discussion

When the standard and probe sequences shared the same duration, participants judged 35% of times the accelerating sequence as lasting longer than the standard and judged 65% of times the decelerating sequence as lasting longer than the standard. These results mimic, both in terms of directionality and magnitude, the biases observed in Experiment 1a. Thus, the mechanism or strategy responsible for the bias equivalently operates across both tested time scales.

These data pose a challenge to change-based models, which otherwise provide a solid theoretical framework in the time-dilation literature. Assuming a change-based perspective would imply that the equal number of changes that defined all sequences (isochronous, accelerating, and decelerating) should theoretically engender equal estimates, while this was not the case. However, a potential way of accommodating the illusion to these accounts would be that the duration biases are determined by the frequency of changes occurring at the beginning of the sequences, i.e., an accelerating sequence which starts with a lower frequency of changes would lead to an underestimation, while a decelerating sequence which starts with a higher frequency of changes would determine an overestimation. We tested this *primacy* explanation in the following experiment, where participants estimated partially pseudo-randomized flicker sequences. This was done to deteriorate the overall pattern of acceleration and deceleration and to isolate the contribution of the initial or final portions of the sequence in establishing the illusion.

Experiment 1c: estimation of scrambled anisochronous flickering visual stimuli

Methods

Participants

Two groups of eight participants each took part in the experiment: Group A (four male; mean age = 28.1, +/− 3.3 years) and Group B (five male; mean age = 26, +/− 2.5 years). All participants gave informed consent and were debriefed on the goals of the experiment once concluded.

Stimuli and task conditions

Groups A and B compared a 1898-ms isochronous standard to a 1898 +/− Δt ms anisochronous probe. We only tested three Δt values for each participant (160 trials where Δt = 0, 40 flanker trials where Δt = 600, and 40 flankers where Δt = −600). Groups A and B compared within each trial an isochronous standard to a *scrambled* accelerating/decelerating anisochronous probe. Scrambled probe sequences were constructed by rearranging in different ways our original accelerating/decelerating sequence intervals.

Group A estimated four types of probes (as a reference, the interval order in Experiment 1a acceleration was 1-2-3-4-5-6-7-8, starting from the longest interval 1 to the shortest interval 8 , while in deceleration the interval order was reversed 8-7-6-5-4-3-2-1).

Primacy-acceleration: Sequences which started with the first interval of an accelerating sequence (the longest pause = lowest frequency), followed by a pseudo-random arrangement of the seven remaining shorter intervals, e.g., 1-4-8-3-7-5-2-6. Four different pseudo-randomized arrangements were used.

Primacy-deceleration: Sequences which started with the first interval of a decelerating sequence (the shortest pause = highest frequency), followed by a pseudo-random arrangement of seven of the remaining longer intervals, e.g., 8-1-5-2-7-4-3-6.

Recency-acceleration: Sequences which started with a pseudo-random arrangement of the first seven longer intervals of an accelerating sequence and finished with the last properly arranged interval (the shortest pause = highest frequency), e.g., 5-4-7-2-1-3-6-8.

Recency-deceleration: Sequences which started with a pseudo-random arrangement of the first seven shorter intervals of a decelerating sequence and finished with the last properly arranged interval (the longest pause = lowest frequency), e.g., 4-2-8-5-3-7-6-1.

Group B performed an identical task to Group A, the only exception being the number (three) of properly arranged intervals at the beginning or end of the sequence, e.g., primacy-acceleration = 1-2-3-8-4-7-5-6; primacy-deceleration = 8-7-6-1-5-2-4-3; recency-acceleration = 5-1-4-2-3-6-7-8; recency-deceleration = 4-8-5-7-6-3-2-1. Thus, across both groups we tested primacy/recency effects testing sequences subject to different degrees of pseudo-randomization.

With the four types of probes we systematically provide subjects with the highest or lowest frequencies at the beginning or end of the sequences while scrambling the remaining intervals, thus partially deteriorating the overall patterns of acceleration or deceleration. The purpose of this manipulation was to assess whether different placements of the highest and lowest frequencies within the sequence (beginning or end) could condition responses in different ways. If we assume that the frequency set at the beginning of the sequence is critical in establishing the illusion, then we should expect a greater dissociation between acceleration and deceleration in the primacy conditions with respect to the recency conditions (i.e., a greater dissociation between the primacy-acceleration and primacy-deceleration probes, opposed to the recency-acceleration and recency-deceleration probes). If on the other hand the bias is determined by the overall pattern of the sequence, then

we should expect equal acceleration/deceleration dissociations in the primacy and recency conditions.

The pseudo-randomized sequences were assembled according to two rules: (a) The first interval following the initial portion of the primacy probes and the interval preceding the final portion of the recency probes could not correspond to the immediately adjacent interval of an accelerating or decelerating sequence (e.g., 1-2-7-4-5-8-3) and (b) Primacy and recency probes never began or finished with the same intervals (e.g., primacy acceleration = 1-4-8-3-7-5-2-6; recency acceleration = 1-4-7-2-5-3-6-8).

Analysis

We analyzed in both groups the proportion of "probe longer" responses for probe sequences with $\Delta t = 0$ (40 primacy-acceleration, 40 primacy-deceleration, 40 recency-acceleration, and 40 recency-deceleration), while excluding from the analysis the remaining probe sequences with $\Delta t = +/-600$, which were treated as flankers.

Results

Group A responses for probe sequences with $\Delta t = 0$ were submitted to a $2 \times 2 \times 2$ factorial ANOVA (Probe Pattern: *accelerating* vs. *decelerating* × High/Low Frequency Placement: *primacy* vs. *recency* × Stimulus Order: *standard-probe* vs. *probe-standard*). The analysis revealed no significant effects of Probe Pattern [$F(1, 6) = 1.299$, p n.s.], no effect of High/Low Frequency Placement [$F(1, 6) = .84$, p n.s.], and no effect of Stimulus Order [$F(1, 6) = 1.65$, p n.s.]. No significant interactions were observed (Figure 3b).

An equivalent analysis on Group B responses to probe sequences with $\Delta t = 0$, showed a significant effect of Probe Pattern [$F(1, 6) = 6.71$, $p < .05$], no effect of High/Low Frequency Placement [$F(1, 6) = .85$, p n.s.], no effect of Stimulus Order [$F(1, 6) = .02$, p n.s.], and no significant interactions. Group B showed the persistence of an acceleration-deceleration dissociation, albeit smaller in amplitude to that observed in Experiment 1a.

Discussion

This experiment revealed two main results: (a) The magnitude of acceleration-deceleration biases is dependent on the degree of scrambling applied to intervals within a sequence. Group A (seven scrambled intervals) showed no significant difference between the perception of accelerating and decelerating sequences, while Group B (five scrambled intervals) showed a small, yet significant, acceleration-deceleration dissociation (Figure 3c). (b) Primacy/recency effects play no significant role in shaping the bias, as duration estimates do not vary depending on the placement of the highest or lowest frequencies within the sequence. Sequences which start with the highest (or lowest) frequencies are equivalently judged to sequences which end with the lowest (or highest) frequencies. The crucial element is that both these sequences never begin with the same intervals (which we made sure of in the pseudo-randomization), yet they produce equal outcomes.

These data highlight that the key factor in determining the bias is the extent to which a participant is capable of recognizing the sequence as accelerating or decelerating. The information necessary to operate this distinction is drawn from the overall pattern of changes occurring throughout the sequence. In this respect, the number of changes occurring at the beginning of the sequence is equally informative to the number occurring at its end.

As previously discussed, the effect uncovered in Experiment 1 might reflect a *spatial displacement* heuristic, where subjects treated stationary accelerating sequences as *objects* that cover ground in less time, whereas decelerating sequences as objects that cover ground in more time. In the following experiment, this phenomenon was studied in a configuration in which the *moving object* scenario was made explicit. Also, adding displacement information enabled the manipulation of time and space independently, thus yielding nonuniform motion by means of anisochronous and/or anisometric dynamics. In this case spatial displacement is added to the equation to verify from a behavioral point of view whether motionless anisochronous flicker and anisometric motion rely on a common form of movement processing. In particular, the aim of Experiment 2 was that of establishing whether: (a) the bias observed in Experiment 1 resembles that associated to the estimation of an actual accelerating/decelerating moving stimulus and (b) the effect can be transposed to the spatial domain (i.e., whether anisotropic displacements and anisochronous draw cycles can produce equivalent behavioral outcomes), thus validating stimulus velocity as the crucial modulating factor.

Experiment 2: effects of anisometric displacements and anisochronous sequencing on the estimated duration of drifting Gabor-patch configurations

Methods

Participants

Eight volunteers with normal or corrected to normal vision participated in the second experiment (two male;

mean age = 26.5, +/− 3.1 years). All participants gave informed consent and were debriefed on the goals of the experiment once concluded.

Stimuli and task conditions

Participants performed a similar forced choice psychophysical task to that of Experiment 1 in which they were required to compare drifting Gabor-patch stimuli endowed with regular dynamics (standard stimulus drifting at a uniform velocity) to equivalent stimuli displaced by means of nonregular dynamics (accelerating or decelerating probe stimulus). Within each trial subjects were sequentially shown two leftward horizontally drifting Gabor-patch animations (standard followed by probe or probe followed by standard, counterbalanced across participants); both stimuli drifted within a static Gaussian aperture, encompassing approximately 12° of visual angle at 57-cm viewing distance (as in Kaneko and Murakami, 2009). A fixation dot was placed approximately 0.6° above the visible extent of the Gabor-patch. Each trial began with the presentation of an acoustic signal which was followed after 750-ms delay by the first drifting stimulus (standard or probe). The second stimulus was presented after a further 1500-ms delay, at the end of which participants had to indicate whether it appeared to last longer or shorter than the first stimulus (response coding was counterbalanced within participants). The next trial began 750 ms after the emitted response. Subjects were instructed to maintain their gaze on the fixation dot throughout the entire extent of the trial.

Both standard and probe stimuli comprised 24 frames of animation. The horizontal sinusoidal grid possessed a constant spatial frequency of 0.77 cpd (cycles per degree). The standard stimulus was characterized by a constant *isochronous* temporal frequency (see Figure 4), where every frame was drawn at a constant rate of 12.6 Hz (i.e., one frame each 79 ms). The total duration of the animation was 1900 ms. Within each frame the grid was *isometrically* shifted by a constant 0.1°of visual angle, thus covering a total phase shift of 2.4°. Given these spatio-temporal characteristics, the standard stimulus drifted at a constant velocity of 1.23°/s. The probe stimulus on the other hand could vary on either the temporal dimension (*anisochronous* frame rate) and/or the spatial dimension (*anisometric* phase shifts across successive frames), thus producing accelerating or decelerating patterns of movement.

Four kinds of probe animations were used in separate experimental sessions, depending on the combination of these two variables (Figure 5).

(a) Anisochrony and Isometry: Draw cycles were progressively shorter or longer, determining *accelerating* and *decelerating* patterns of motion respectively, while the grid drifted a constant number of degrees per draw cycle (Figure 4a). In accelerating probes, the intervals defining the amount of time each frame would remain on screen was obtained by sampling $f(x) = (-0.5x^3 + 13.5x^2 - 121.5x + 464.5)/2.2298$ [x = 1 through 8, at intervals of 0.3; total = 24 samples]; the inter-frame-intervals of the decelerating probe stimuli used the same values of $f(x)$ sampled in the opposite order [x = 8 through 1, at intervals of −0.3] (Figure 4a). The rate of change in this function was identical to that used to generate the anisochronous interstimulus intervals used in Experiment 1; it was obtained by performing a cubic fit of the latter function, resampling for 24 pauses, and downscaling by a factor of 2.2298 so the sum of all pauses was 1900 ms. The total duration of the probe stimulus was 1900 +/− Δt (Δt = 0, 200, 400, and 600 ms), obtained by adding or subtracting a constant ($c = \Delta$ t/24) to each time sample. Thus, the duration of a probe sequence was achieved by varying the amount of time a frame persisted on screen. The probe stimulus covered a constant amount of space per frame of animation (0.1° per frame). Therefore, following the same logic adopted in Experiment 1, the mean temporal frequency (and velocity) of probe and standard stimuli were identical. For example, an accelerating probe stimulus started with a lower velocity than the standard stimulus, while it terminated with a higher velocity (and vice versa for a decelerating probe): the average temporal frequency, average velocity, and the total amount of space covered by these two stimuli was, however, identical. This experimental condition was fundamentally equivalent to the anisochronous sequences of Experiment 1, the only addition being the presence of horizontal isometric drift.

(b) Isochrony and Anisometry: Isochronous and anisotropic probe. Draw cycles were constant, while the grid drifted by a progressively increasing or decreasing number of degrees per draw cycle, determining an *accelerating* and *decelerating* probe, respectively. The degrees of phase shift per frame were calculated by sampling $f(x) = (-0.5x^3 + 13.5x^2 - 121.5x + 464.5)/403.8686$, for x = 8 to 1 at −0.3 intervals (accelerating probe, see Figure 5b), and for x = 1 to 8 at 0.3 intervals (decelerating probe). The total number of degrees shifted was in all cases 2.4°. Within each trial the probe stimulus' duration was 1900 +/− Δt. Therefore, in this experimental condition, acceleration and deceleration were achieved by manipulating the amplitude of spatial displacements (phase shifts) in the course of the animation while the temporal interval between

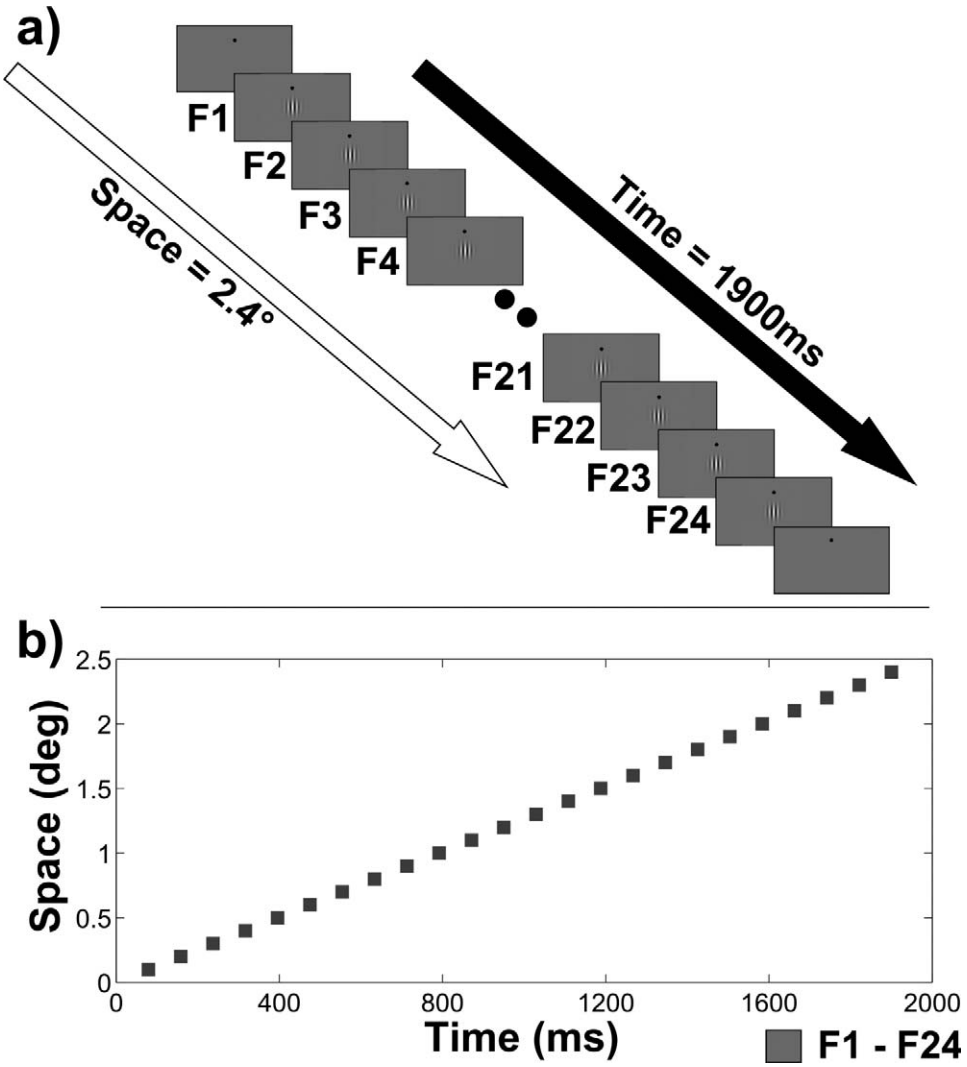

Figure 4. Experiment 2 standard sequence animation (endowed with isochronous and isometric dynamics). The sequence comprises 24 frames which are presented at regular temporal intervals. In each frame the grid drifts by a constant amount of degrees. The standard had a total duration of 1900 ms.

frames was kept constant, hence achieving irregular drifting dynamics in the spatial domain alone.

(c) Anisochrony + Anisometry: Both dimensions vary congruently determining *accelerating* and *decelerating* probe stimuli with a greater degree of variation. In this case for example, an accelerating probe is achieved by means of progressively shorter draw cycles and progressively larger phase shifts, while a decelerating probe results from progressively shorter draw cycles and progressively larger phase shifts (Figure 5c). This was carried out to assess how timing estimates respond to the joint effects of spatial and temporal irregularity. The degree of anisochrony and anisometry are identical to that in sessions a and b. The combined presence of these two variables, however, determines a greater degree of angular acceleration/deceleration. If participants rely on one or the other dimension to formulate predictions of stimulus duration, then we should observe biases in the same order of magnitude as those recorded in sessions a or b. If participants on the other hand rely on both these dimensions to draw conclusions, then biases should be increased with respect to sessions a and b.

(d) Anisochrony – Anisometry: Both dimensions vary incongruently, thus resulting in a regular displacement dynamic (as the standard would appear). For example, a probe might either result from progressively shorter draw cycles and progressively smaller phase shifts (*iso* 1), or, progressively longer draw cycles and progressively larger phase shifts (*iso* 2; see Figure 5d). This was performed in order to assess if the spatial and temporal domains have the same or different weights in determining the illusion, which would result in cancellation or persistence of a probe duration bias.

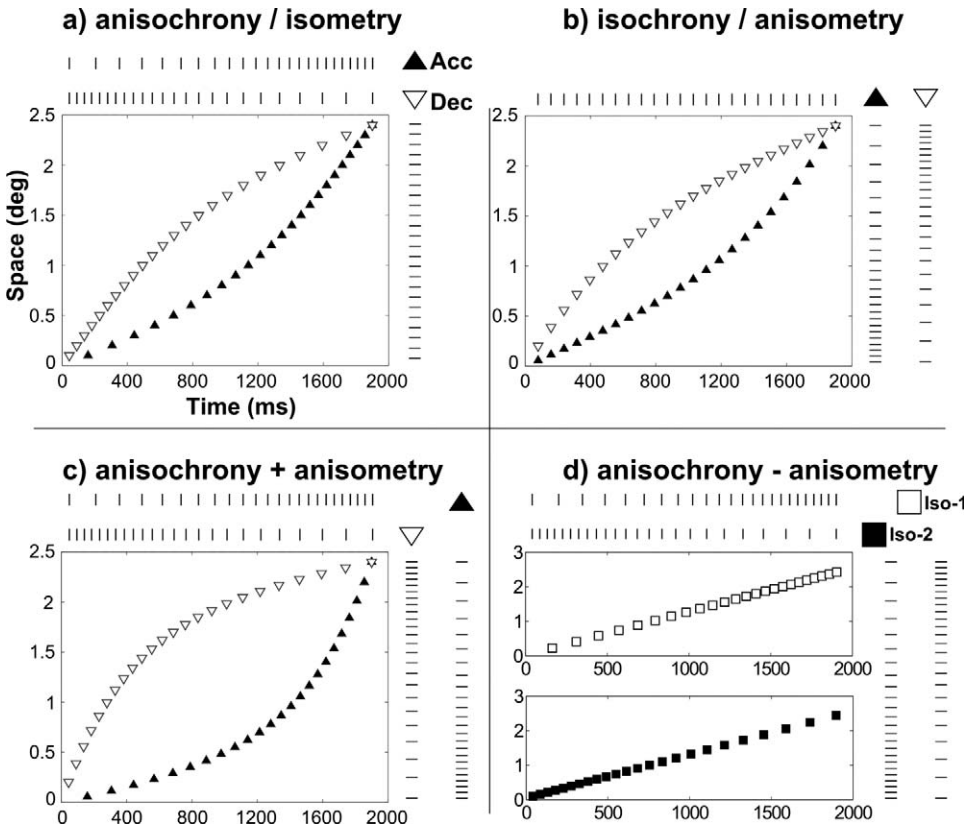

Figure 5. Experiment 2 Probe sequence spatio-temporal dynamics. Acceleration / deceleration is achieved by means of irregular frame rates (anisochrony) and/or irregular degrees of grid phase-shift (anisometry): (a) anisochrony only, (b) anisometry only, (c) congruent anisochrony and anisometry, and (d) incongruent anisochrony and anisometry. The probe sequence duration varied between 1300 ms and 2500 ms.

Each subject performed 40 repetitions per probe type (2 sequence types × 7 Δt values × 4 experimental sessions), for a total of 1,120 trials.

Analysis

Single subject and pooled data were fitted with a logistic psychometric function. The resulting values of parameters alpha and beta were compared across accelerating and decelerating probes in order to identify shifts in PSE and/or variations in sensitivity consequent to anisochrony and/or anisometry established in conditions a through c.

Results

A pooled subject data logistic fit revealed effects similar to those uncovered in the previous experiment: Accelerating and decelerating probes yielded opposite modulatory outcomes on perceived stimulus duration (underestimation and overestimation, respectively). This was clearly evident in all experimental conditions aside the *anisochrony* − *anisometry* condition (Figure 6).

Participants' alpha values were entered into a 4 × 2 repeated measures ANOVA (Session: *anisochrony*/*isometry* vs. *isochrony*/*anisometry* vs. *anisochrony* + *anisometry* vs. *anisochrony* − *anisometry* × Probe Sequence: *accelerating* vs. *decelerating*) which revealed a borderline effect of session [$F(3, 21) = 2.63$, $p = .077$], a significant effect of probe sequence [$F(1, 7) = 14.945$, $p < .01$], and a significant Session × Probe Sequence interaction [$F(3, 21) = 6.22$, $p < .01$] (Figure 7). Fisher LSD post-hoc comparisons were performed to explore this interaction; accelerating and decelerating probes differed within the (a) *anisochrony*/*isometry*, (b) *isochrony*/*anisometry*, and (c) *anisochrony* + *anisometry* sessions [$p < .05$ in all cases], while no difference was observed in the (d) *anisochrony* − *anisometry* session [$p = .78$], where the iso 1/iso 2 probe bias was cancelled out. Underestimations were significantly higher for accelerating probes in the (c) *anisochrony* + *anisometry session* than in the (a) *anisochrony*/*isometry session* [$p < .05$], thus suggesting a cumulative effect of irregular spatial and temporal dynamics. Strangely however, accelerating probe underestimations in the (b) *isochrony*/*anisometry* session were higher than those

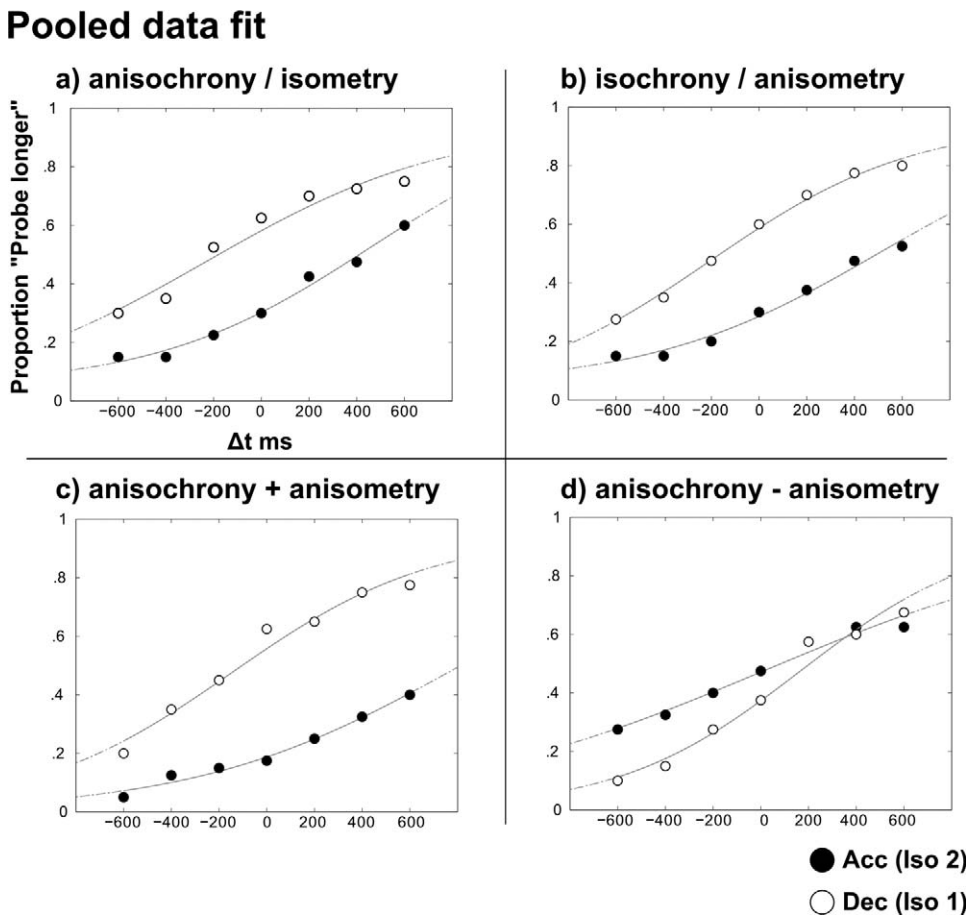

Figure 6. Experiment 2 accelerating and decelerating probe pooled subject logistic fit.

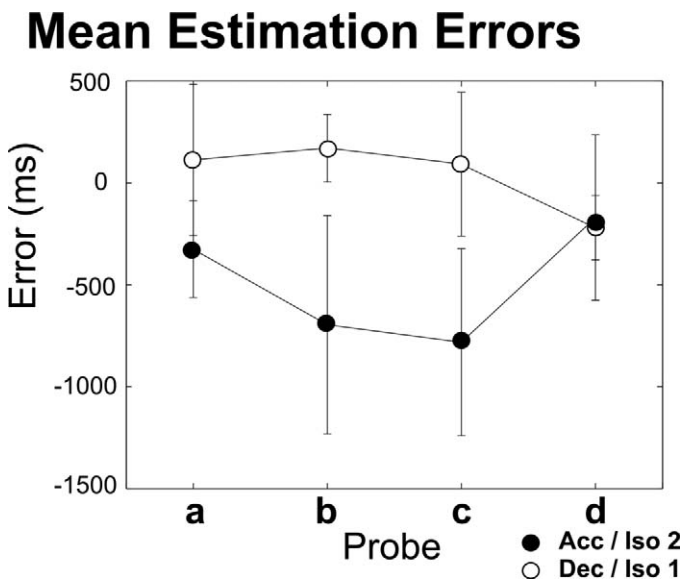

Figure 7. Experiment 2 Mean Estimation errors (positive values = overestimation; negative = underestimation; i.e., error = -PSE) within the: (a) anisochrony / isometry, (b) isochrony / anisometry, (c) anisochrony + anisometry, (d) anisochrony – anisometry probe conditions.

observed in the (a) *anisochrony/isometry* session [$p < .05$], which was not expected. Apparently, spatial anisometry was more effective in producing underestimation in accelerating probes than temporal anisochrony. On the other hand no significant differences between decelerating probes were observed between (a) *anisochrony/isometry*, (b) *isochrony/anisometry*, and (c) *anisochrony + anisometry* sessions.

An equivalent 4 × 2 factorial ANOVA was performed on single subject beta values. No significant main effects or interactions were recorded.

Discussion

The overall effects recorded in this experiment seem to both mimic those of Experiment 1 and extend those observations to displaced stimuli endowed with non-uniform dynamics. The anisochrony probes (a) were derived from the anisochronous sequences utilized in Experiment 1, with the addition of the spatial layer conveying displacement information. As in Experiment 1, acceleration was obtained by a nonlinear distribution of sequences of stimuli (frames) in time. The observed timing biases for accelerating and decelerating stimuli

were analogous in size and directionality to those observed in Experiment 1. Equivalent biases were observed when acceleration resulted from anisometric grid phase shits across temporally constant draw cycles (b), thus confirming that the effect was not confined to the processing of a single dimension subtending visual motion, but responded equally to spatial and temporal indices of visual displacement. The underestimation associated to accelerating probes in the anisometry (b) session was significantly larger than that observed for the anisochony (a) session: apparently, acceleration produced by means of nonuniform spatial displacements evokes stronger biases than an equivalent acceleration determined by means of nonuniformly timed changes in space. The reason subtending this dissociation is however unclear and was not predicted. In the anisochrony + anisometry (c) session, acceleration was achieved by the joint presence of temporal and spatial irregularity. This resulted in larger underestimation of accelerating probe stimuli with respect to the anisochrony (a), but not the anisometry (b) session. The increased effect (with respect to session (a) is explainable in terms of the higher angular acceleration of these probe stimuli. This is depicted in Figure 5 in which each probe is represented in terms of the spatial (y) and temporal (x) evolution it encounters in the course of an animation (24 frames, covering 2.4° in 1900 ms). The slope (y/x ratio) of each curve indicates the average angular velocity which is constant across all conditions and is equivalent to constant angular velocity of the standard. The rate of change (i.e., the curvature, indicating the change in angular velocity between successive frames) indicates angular acceleration, which is greater in the anisochrony + anisometry session. Also in this case we have indication that the apparent duration bias depends on the combined effect of temporal and spatial indices; if this effect would have relied exclusively on temporal irregularity, then the spatial irregular information would have been neglected, thus resulting in an equivalent perceptual bias to that of the anisochrony session. This information is also available in the anisochrony − anisometry session, where the lack of an effect (equivalent biases for accelerating and decelerating probes) indicates an integration of both spatial and temporal acceleratory indices. By combining temporally accelerating and spatially decelerating dynamics (and vice versa), the apparent angular velocity remains constant (i.e., angular acceleration = 0), thus determining the perception of a regularly displaced stimulus.

Curiously, the effects observed for accelerating and decelerating probes were not symmetrical. Overestimations consequent to decelerating probes were smaller in magnitude and did not significantly vary across the different conditions. Apparently, accelerating stimuli trigger stronger underestimation biases than the overestimation determined by equivalent decelerating stimuli.

As previously stated, a likely neuroanatomical source of the classic time dilation effect presumably was in area MT/V5, given the joint modulatory effects of spatial and temporal frequency (Kaneko & Murakami, 2009). Since MT/V5 response is attenuated in presence of isoluminant stimuli (Gegenfurtner & Hawken, 1996; Gegenfurtner et al., 1994), in the following experiment we explored whether the temporal illusion induced by anisochronous sequences of stationary flickering stimuli, is reduced by setting the stimuli at isoluminant levels with respect to the background.

Experiment 3: effects of anisochronous sequencing on the estimated duration of isoluminant stationary flickering

Methods

Participants

Eight volunteers with normal or corrected to normal vision participated in the experiment (two male; mean age = 26.4, +/− 2.2 years). All participants gave informed consent and were debriefed on the goals of the experiment once concluded.

Stimuli and task conditions

Participants carried out within two separate experimental sessions an identical task to that performed in Experiment 1: in one session, red stationary flickering stimuli were presented at nonisoluminant levels with respect to a green background (baseline session; equivalent to Experiment 1), whereas in another session, equivalent stimuli were set at isoluminant levels with respect to the background (isoluminant session). The order of conditions (first baseline–second isoluminant, or vice versa) and the order of stimuli within each trial (first standard–second probe, or vice versa) were counterbalanced across participants. Each participants performed 40 repetitions per probe type (2 sequence types × 7 Δt values × 2 experimental sessions), for a total of 1120 trials. The task was performed in a dimly lit room, with a fixed level of environmental luminosity. The stimulus intensity required for stimulus-background equiluminance was set for each participant in a preliminary testing session in which a red circular stimulus (radius = 2° of visual angle at 57-cm viewing distance) was presented intermittently over a green background at a 15-Hz flicker rate (Kelly,

1983). Participants had to manually adjust the intensity of the red stimulus until the flicker rate became impossible to discern (i.e., flickering appeared to cease). Only intensity of the red channel was modulated. Subjects repeated this task 10 times: the average intensity value was tested to confirm it yielded the intended effect and was subsequently used in the *isoluminant condition*. In the nonisoluminant condition, the luminance of red stimuli was set at a fixed value—approximately 35% higher luminance than the average value of isoluminant stimuli across all participants. This value was chosen arbitrarily; we simply chose a value which was well above the equiluminance threshold of all participants. This value was empirically tested at the beginning of each participant's session as to assure that it did not appear equiluminant. Both the nonisoluminant and isoluminant conditions were procedurally identical to Experiment 1a, with the only exception being the absence of control isochronous sequences. All relevant information was drawn from the comparison of equivalent anisochronous gradients across the isoluminant and nonisoluminant conditions.

Analysis

Single subject and pooled subject data were fitted with a logistic psychometric function. The resulting values of alpha and beta were compared across accelerating/decelerating anisochronous sequences within the nonisoluminant and isoluminant conditions.

Results

A pooled data logistic fit revealed, in both the baseline (nonisoluminant) and isoluminant conditions, opposite effects of accelerating and decelerating probe sequences on timing estimates (baseline: accelerating PSE = 146-ms underestimation vs. decelerating PSE = 168-ms overestimation; isoluminant: accelerating PSE = 180-ms underestimation vs. decelerating PSE = 177-ms overestimation; Figure 8a).

A 2 × 2 × 2 × 2 factorial ANOVA (Session Order: *baseline-isoluminant* vs. *isoluminant-baseline* × Stimulus Order: *standard-probe* vs. *probe-standard* × Experimental Session: *baseline* vs. *isoluminant* × Probe Sequence: *accelerating* vs. *decelerating*) performed on participant's alpha values (PSE), revealed a significant main effect of Probe Sequence [$F(1, 4) = 46.15$, $p < 0.01$; Figure 8b], and no significant main effects of Session Order [$F(1, 4) = 0.07$, p n.s.], Stimulus Order [$F(1, 4) = 0.14$, p n.s.], and Experimental Session [$F(1, 4) = 0.03$, p n.s.]. No significant interactions were recorded. The lack of an Experimental Session significant main effect and the absence of a significant Probe Sequence × Experimental Session interaction clearly demonstrate that setting stimuli at isoluminant levels with the background proved ineffectual in affecting the intensity of the illusion.

An equivalent 2 × 2 × 2 × 2 factorial ANOVA performed on participants' beta values, revealed a significant Experimental Session × Session Order interaction [$F(1, 4) = 8.46$, $p < 0.05$]. LSD post-hoc analysis revealed that this was due to a higher sensitivity to change in stimulus duration (lower beta values) in the isoluminant session when it was the first experimental session to be carried out. The reason behind this interaction is unclear; despite this, this result has no bearing on the lack of a modulatory effect of stimulus/background luminance contrasts on time estimation performance.

Discussion

As observed in Experiment 1, decelerating and accelerating probe stimuli of equivalent physical duration yielded opposite duration estimates: this dissociation held true both when stimuli were set to isoluminant (flicker rate was detectable exclusively by means of chromatic contrast) and nonisoluminant levels with respect to the background. Area MT/V5, which represents a processing stage along the dorsal motion pathway, receives its primary input from the subcortical M channel which mostly responds to luminance (J. Maunsell, Nealey, & DePriest, 1990; J. H. R. Maunsell & Newsome, 1987; Mishkin, Ungerleider, & Macko, 1983; Ungerleider, Mishkin, Ingle, Goodale, & Mansfield, 1982; Van Essen, 1985). A number of psychophysical (Cabanagh & Anstis, 1991; Lindsey & Teller, 1990; Mullen & Boulton, 1992) and physiological studies (Charles & Logothetis, 1989; K. Dobkins & Albright, 1990; K. R. Dobkins & Albright, 1994; Saito, Tanaka, Isono, Yasuda, & Mikami, 1989) demonstrate that several aspects of motion perception are preserved with isoluminant stimuli; this works against a strict separation in the neural substrates responsible for color and motion processing. Having said that, recordings in macaque MT neurons do however show attenuated responses to drifting isoluminant gratings . The same authors also point out that the MT neurons which respond to isoluminant stimuli do so in an inconsistent manner; moreover, only intensely modulated targets are capable of evoking a response, thus denoting reduced contrast sensitivity in this neuronal subpopulation.

Considering these findings, it would be reasonable to assume that if activity in area MT were critical for the illusion, then stimulus isoluminance should be expected to have at least some impact on the amplitude of the bias. Since our results show no attenuation in the effect, we can theoretically state that the source of the bias is

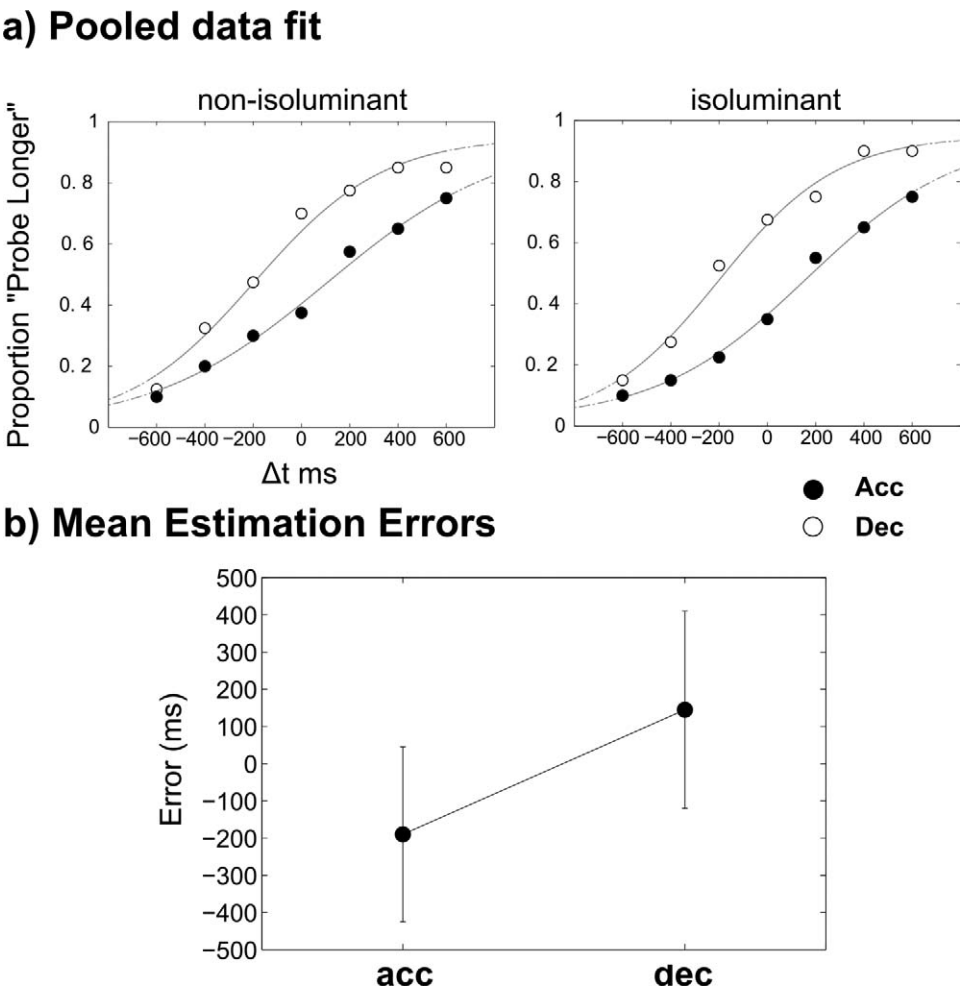

Figure 8. Nonisoluminant and isoluminant condition pooled subject logistic fit and estimation error values (-PSE).

not located in area MT. The source of this effect might therefore lie in higher hierarchical levels of motion processing onto which both M and P channel inputs converge. Perhaps the effect is not exclusive to the visual modality and reflects cross-modal or amodal representations of stimulus motion dynamics. However, in the absence of direct physiological data, this conclusion remains largely hypothetical since stimulus isoluminance only provides us with an indirect tool of assessing the involvement of area MT in establishing the bias. Aside this, these results enable us to establish that the illusion is not exclusively dependent on luminance based contrast.

General Discussion

As evidenced in the present paper, largely symmetrical time dilation and time contraction phenomena can be achieved by manipulating the temporal and/or spatio-temporal sequencing of visual stimuli independently of the amount of overall information delivered. To our knowledge, this represents a new finding within the human timing literature; we refer to this illusory effect with the acronym ATI (Aniso-Time-Illusion). In all experiments this was achieved by means of anisochronous and/or anisometric dynamics of stimulus variation, yielding progressively increasing or decreasing flicker rates (Experiments 1a, 1b, and 3) and accelerating or decelerating patterns of horizontal displacement (Experiment 2).

With respect to previous experimental accounts concerning the classic time-dilation effect, the present results thus seem to highlight a more *subtle* relationship between the spatio-temporal evolution of a dynamic visual event and the estimated time the event takes to unfold: a positive or negative sign of change in hertz or angular velocity—opposed to higher or lower hertz or angular velocity—was systematically equated to stimulus duration. A possible interpretation is that these symmetric, organized, and distinctively motion-related patterns evoked some form of heuristic in the line of *accelerating object = covers ground in less time* whereas *decelerating object = covers ground in more time* associations. In Experiment 1, the visual system was

fed with fractional motion information, which was however sufficient in evoking an equivalent response to that associated to the horizontally displaced stimuli adopted in Experiment 2. Therefore participants equivalently judged stationary flickering and horizontally drifting stimuli based on the commonality of their dynamics. The crucial factor was not represented by the temporal sequencing of stimuli, since an identical effect could be achieved by means of temporally regular/spatially irregular displacements (Experiment 2: isochrony and anisometry probe), thus highlighting the key role of actual stimulus velocity or velocity information *derived* from partial motion indices. Therefore the overlapping results obtained in Experiments 1 and 2 were likely due to participants treating flickering stationary stimuli as *moving* objects with progressively increasing or decreasing *velocity*. This is likely the result of an acquired association between spatial and temporal dynamics characterizing kinematics in an ecological setting. The results of our study crucially demonstrate that, due to these learnt associations, the isolated presentation of temporal dynamics are capable of evoking the same subjective timing experiences that are usually triggered by specific combinations of temporal and spatial dynamics.

While the classical time-dilation effect could be theoretically linked to area MT/V5, the same may not apply to the present time-dilation/time-contraction results, since no timing estimate modulations were observed when flickering stimuli were set at isoluminant levels with respect to the background (Experiment 3). This hypothetically places the source of the effect upstream in an area in which luminance and chromatic contrast information are both available. This illusion could theoretically reflect the exploitation of cross-modal/amodal representations of stimulus motion dynamics if equivalent results were observable across different sensory modalities.

Change based accounts of time indexing cannot account for such results since all manipulated dimensions—frame rate (Experiments 1, 2, anisochrony conditions, and Experiment 3), spatial displacement, and angular velocity (Experiment 2)—were subject to overall equal amounts of changes. However a possible explanation would have been that changes occurring at the beginning of the sequence have a greater salience than those occurring at the end of the sequence. Experiment 1c, however, showed that the factor which best described subject performance was the overall pattern of changes, and the extent to which this pattern could be recognized as acceleration or deceleration. Local primacy (and recency) effects were incapable of providing a valid explanation for the effect.

A consolidated framework used to model timekeeping performance is provided by the *Internal Clock* model (Church, 1984; Treisman, 1963), where an internal oscillator is assumed to emit pulses at a regular rate. When evaluating a stimulus, clock pulses are accumulated throughout its period of presentation; the perceived duration of the stimulus is proportional to the total number of pulses accumulated between its onset and offset. According to this framework, distortions in time perception can be explained in terms of inconsistencies in clock frequency determined by specific experimental manipulations. A stimulus which increases clock frequency will engender a greater number of accumulated pulses and an overestimated account of subjective duration. A way of accommodating the results of this study to the operation of an internal clock would be that acceleration and deceleration produce asymmetrical rates of change in clock frequency. In reference to the Internal Clock hypothesis, we know that higher velocities determine higher clock frequencies while lower velocities determine lower clock frequencies; what we don't know is whether the rate with which clock frequency varies in response to a transition from a higher to a lower velocity is equivalent to that elicited by the transition from a lower to a higher velocity. If the rate of change in clock frequency is not equal between acceleration and deceleration, then the overall amount of accumulated clock pulses will differ between these two conditions. In our study decelerating stimuli were overestimated with respect to controls, while accelerating stimuli were underestimated: it could be that a transition from a higher to a lower velocity (deceleration) determines a slower drop in clock pulses than the rate of increase in clock pulses occurring when the transition in velocities is reversed (acceleration). Put in simple terms this would mean that clock frequency takes more time to slow down during deceleration than it takes to speed up during acceleration. The average clock frequency during deceleration would therefore be higher than the average clock frequency in presence of acceleration, thus explaining why it appears to last longer.

Otherwise, these asymmetrical timing biases could reflect heuristic strategies aimed at favoring the efficiency of interactions with visual targets characterized by nonuniform patterns of motion. In the context of subject–target interactions, acceleration and deceleration could lead to different biases. Approaching accelerating targets could lead to a *behaviorally conservative* underestimation, which in turn triggers an anticipatory avoidance behavior. This would be an ecologically plausible strategy. However, the reason why a decelerating stimulus would be overestimated is hard to grasp from an ecological standpoint. This interpretation is however conjectural since the task was not explicitly interactive: judgments were retrospective and stimuli were either spatially invariant (Experiments 1 and 3) or moving on the fronto-parallel plane (Experiment 2) as opposed to motion on the sagittal

plane (as typical in subject/object interactions). Also, several studies show that looming stimuli engender time expansion (Lin, Franconeri, & Enns, 2008; Van Wassenhove, Buonomano, Shimojo, & Shams, 2008). This would seem to work against the idea that subjects in our experiment translated an accelerating stationary stimulus into a *looming* stimulus (i.e., acceleration produced time compression, not expansion).

Several studies emphasize the notion of the nervous system as an active predictor of patterns of sensory information based on currently incoming spatio-temporal cues (Enns & Lleras, 2008; Mumford, 1992; Rao & Ballard, 1999). Recent accounts show how the visual system extrapolates and predicts the spatial pattern (phase and orientation of drifting periodic stimuli) of expected incoming visual inputs (Roach, McGraw, & Johnston, 2011), or how spatio-temporal information are extracted from displaced visual stimuli to estimate trajectory and velocity (O'Reilly, Mesulam, & Nobre, 2008). We could theorize that our data relates in some measure to these findings. When we observe a travelling object our brain can exploit acquired associations of spatio-temporal environmental regularities to predict spatial and temporal coordinates that the object will occupy in the future. This implies that the retrospective *offline* timing estimates subjects provided in our study could be based on these associations, which are typically used by the brain to make *online* predictions during the active interaction of the organism with the environment.

Another potential explanation for the illusion could be provided by the State-Dependent Network model (Buonomano, 2005; Buonomano et al., 2009; Karmarkar & Buonomano, 2007). This model predicts that cortical networks are inherently capable of coding time information as a function of time dependent changes in network state. Given that our accelerating-decelerating stimuli consist in symmetrical arrangements of the same stimuli, then this model would effectively predict different network state outcomes. Accelerating and decelerating rates of stimulus presentation would interact differently with the time-windows required for the network to reset to its previous state, thus determining different outcomes at the end of the sequence. While this model potentially explains why different arrangements of the same stimuli lead to different perceptual outcomes, it cannot explain why acceleration leads to underestimations while decelerations lead to overestimations (respect to an isochronous control). Network states are essentially *tags* arbitrarily associated to physical durations; the state in itself contains no explicit quantitative metric of time (opposed to how the clock model hypothesizes that greater number of accumulated pulses code for longer elapsed time). Thus this model explains why different stimuli appear to differ in duration, but not why one stimulus is perceived longer than the other.

The patterns of flicker and/or displacement here described represent spatio-temporal *gestalts*, where the same amount of raw sensory information—arranged in different ways defining patterns of accelerating and decelerating motion—lead to diametrically opposite time estimation errors. The crucial information required to produce accurate estimations of stimulus duration is provided by the time of onset and offset of stimulation; monitoring the passage of time separating these two events is sufficient to perform the task, while all intermediate events occurring within this span should be deemed irrelevant. Despite this fact, subjects clearly exploit the arrangement of this redundant information, using it to construct a prediction of overall stimulus duration. This influence is common to both the present data concerning nonuniform dynamics, as well as the *classical* time-dilation effect obtained by means of isometric dynamics—and more in general all manipulations related to the filled-duration illusion—in which the number of intermediate changes affects the perception of the overall duration of a period of stimulation. Despite not being informative of stimulus duration, subjects probably relied in the present experiments on the nonuniform structure of stimulation given its distinct resemblance to coherent patterns of displacement. These patterns capture a common ecological *rule* of dynamics to which objects (and agents) in our environment are commonly subject to (i.e., objects accelerate when falling, animals accelerate to achieve a desired velocity and decelerate to stop; in general, all events are subject to variable dynamics). Future efforts should be made to identify other kinds of nonuniform dynamics that affect duration estimation, and understand what advantages (assuming there are any) organisms gain by exploiting them.

Conclusions

In the present paper we demonstrated how nonuniformly arranged visual events in time, and in time and space systematically lead to biased time estimations (ATI: Aniso-Time-Illusion). Symmetrical accelerating and decelerating stationary flicker patterns and horizontally displaced visual stimuli, respectively, produced time contraction and time dilation phenomena. These stimuli were created by arranging in opposite ways the same amount of raw sensory information; the resulting effects highlighted how timing biases may respond to the way information is delivered in time, opposed to the overall quantity of information that characterizes a

stimulus as observable in experimental contexts related to the classical filled-duration illusion.

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References

Brown, S. W. (1995). Time, change, and motion: The effects of stimulus movement on temporal perception. *Perception and Psychophysics, 57*(1), 105–116.

Buonomano, D. V. (2005). A learning rule for the emergence of stable dynamics and timing in recurrent networks. *Journal of Neurophysiology, 94*(4), 2275–2283.

Buonomano, D. V., Bramen, J., & Khodadadifar, M. (2009). Influence of the interstimulus interval on temporal processing and learning: Testing the state-dependent network model. *Philosophical Transactions of the Royal Society B: Biological Sciences, 364*(1525), 1865.

Cabanagh, P., & Anstis, S. (1991). The contribution of color to motion in normal and color-deficient observers. *Vision Research, 31*(12), 2109–2148.

Charles, E., & Logothetis, N. (1989). The responses of middle temporal (MT) neurons to isoluminant stimuli. *Investigative Ophthalmology & Visual Science, 30*, 427.

Church, R. M. (1984). Properties of the internal clock. *Annals of the New York Academy of Sciences, 423*, 566–582.

Dobkins, K., & Albright, T. (1990). Color facilitates motion correspondence in visual area MT [Abstract]. *Society for Neuroscience Abstracts, 16*, 1220.

Dobkins, K. R., & Albright, T. D. (1994). What happens if it changes color when it moves?: The nature of chromatic input to macaque visual area MT. *The Journal of Neuroscience, 14*(8), 4854–4870.

Enns, J. T., & Lleras, A. (2008). What's next? New evidence for prediction in human vision. *Trends in Cognitive Sciences, 12*(9), 327–333.

Gegenfurtner, K. R., & Hawken, M. J. (1996). Interaction of motion and color in the visual pathways. *Trends in Neurosciences, 19*(9), 394–401.

Gegenfurtner, K. R., Kiper, D. C., Beusmans, J. M. H., Carandini, M., Zaidi, Q., & Movshon, J. A. (1994). Chromatic properties of neurons in macaque MT. *Visual Neuroscience, 11*, 455–455.

Goldstone, S., & Lhamon, W. T. (1974). Studies of auditory-visual differences in human time judgment. 1. Sounds are judged longer than lights. *Perceptual and Motor Skills, 39*(1), 63–82.

Kanai, R., Paffen, C. L., Hogendoorn, H., & Verstraten, F. A. (2006). Time dilation in dynamic visual display. *Journal of Vision, 6*(12):8, 1421–1430, http://www.journalofvision.org/content/6/12/8, doi:10.1167/6.12.8. [PubMed] [Article]

Kaneko, S., & Murakami, I. (2009). Perceived duration of visual motion increases with speed. *Journal of Vision, 9*(7):14, 1–12, http://www.journalofvision.org/content/9/7/14, doi:10.1167/9.7.14. [PubMed] [Article]

Karmarkar, U. R., & Buonomano, D. V. (2007). Timing in the absence of clocks: Encoding time in neural network states. *Neuron, 53*(3), 427–438.

Kelly, D. (1983). Spatiotemporal variation of chromatic and achromatic contrast thresholds. *Journal of the Optical Society of America, 73*(6), 742–749.

Lin, J. Y., Franconeri, S., & Enns, J. T. (2008). Objects on a collision path with the observer demand attention. *Psychological Science, 19*(7), 686.

Lindsey, D. T., & Teller, D. Y. (1990). Motion at isoluminance: Discrimination/detection ratios for moving isoluminant gratings. *Vision Research, 30*(11), 1751–1761.

Maunsell, J., Nealey, T. A., & DePriest, D. D. (1990). Magnocellular and parvocellular contributions to responses in the middle temporal visual area (MT) of the macaque monkey. *The Journal of Neuroscience, 10*(10), 3323.

Maunsell, J. H. R., & Newsome, W. T. (1987). Visual processing in monkey extrastriate cortex. *Annual Review of Neuroscience, 10*(1), 363–401.

Mishkin, M., Ungerleider, L. G., & Macko, K. A. (1983). Object vision and spatial vision: Two

cortical pathways. *Trends in Neurosciences, 6*, 414–417.

Mullen, K., & Boulton, J. C. (1992). Absence of smooth motion perception in color vision. *Vision Research, 32*(3), 483–488.

Mumford, D. (1992). On the computational architecture of the neocortex. *Biological Cybernetics, 66*(3), 241–251.

Näätänen, R., Syssoeva, O., & Takegata, R. (2004). Automatic time perception in the human brain for intervals ranging from milliseconds to seconds. *Psychophysiology, 41*(4), 660–663.

O'Reilly, J. X., Mesulam, M. M., & Nobre, A. C. (2008). The cerebellum predicts the timing of perceptual events. *Journal of Neuroscience, 28*(9), 2252–2260.

Pariyadath, V., & Eagleman, D. (2007). The effect of predictability on subjective duration. *PLoS One, 2*(11), 1264.

Perrone, J. A., & Thiele, A. (2001). Speed skills: Measuring the visual speed analyzing properties of primate MT neurons. *Nature Neuroscience, 4*(5), 526–532.

Priebe, N. J., Lisberger, S. G., & Movshon, J. A. (2006). Tuning for spatiotemporal frequency and speed in directionally selective neurons of macaque striate cortex. *The Journal of Neuroscience, 26*(11), 2941.

Rammsayer, T. H. (1999). Neuropharmacological evidence for different timing mechanisms in humans. *The Quarterly Journal of Experimental Psychology: Section B, 52*(3), 273–286.

Rammsayer, T. H., & Lima, S. D. (1991). Duration discrimination of filled and empty auditory intervals: Cognitive and perceptual factors. *Attention, Perception, & Psychophysics, 50*(6), 565–574.

Ranganath, C., & Rainer, G. (2003). Neural mechanisms for detecting and remembering novel events. *Nature Reviews Neuroscience, 4*(3), 193–202.

Rao, R. P. N., & Ballard, D. H. (1999). Predictive coding in the visual cortex: A functional interpretation of some extra-classical receptive-field effects. *Nature Neuroscience, 2*, 79–87.

Roach, N. W., McGraw, P. V., & Johnston, A. (2011). Visual motion induces a forward prediction of spatial pattern. *Current Biology, 21*(9), 740–745.

Roelofs, C. O., & Zeeman, W. P. C. (1951). Influence of different sequences of optical stimuli on the estimation of duration of a given interval of time. *Acta Psychologica, 8*, 89–128.

Saito, H., Tanaka, K., Isono, H., Yasuda, M., & Mikami, A. (1989). Directionally selective response of cells in the middle temporal area (MT) of the macaque monkey to the movement of equiluminous opponent color stimuli. *Experimental Brain Research, 75*(1), 1–14.

Treisman, M. (1963). Temporal discrimination and the indifference interval: Implications for a model of the "internal clock." *Psychological Monographs, 77*(13), 1–31.

Tse, P. U., Intriligator, J., Rivest, J., & Cavanagh, P. (2004). Attention and the subjective expansion of time. *Perception and Psychophysics, 66*(7), 1171–1189.

Ulrich, R., Nitschke, J., & Rammsayer, T. (2006). Perceived duration of expected and unexpected stimuli. *Psychological Research, 70*(2), 77–87.

Ungerleider, L., Mishkin, M. (1982). In D. Ingle, M. Goodale, & R. Mansfield (Eds.), *Analysis of Visual Behavior* (pp. 549–586). Cambridge, MA: The MIT Press.

Van Essen, D. C. (1985). Functional organization of primate visual cortex. *Cerebral Cortex, 3*, 259–329.

Van Wassenhove, V., Buonomano, D. V., Shimojo, S., & Shams, L. (2008). Distortions of subjective time perception within and across senses. *PLoS One, 3*(1), e1437.

Wichmann, F. A., & Hill, N. J. (2001a). The psychometric function: I. Fitting, sampling, and goodness of fit. *Perception & Psychophysics, 63*(8), 1293–1313.

Wichmann, F. A., & Hill, N. J. (2001b). The psychometric function: II. Bootstrap-based confidence intervals and sampling. *Perception & Psychophysics, 63*(8), 1314–1329.

Witherspoon, D., & Allan, L. G. (1985). Time judgments and the repetition effect in perceptual identification. *Memory and Cognition, 13*, 101–111.

Xuan, B., Zhang, D., He, S., & Chen, X. (2007). Larger stimuli are judged to last longer. *Journal of Vision, 7*(10):2, 1–5, http://www.journalofvision.org/content/7/10/2, doi:10.1167/7.10.2. [PubMed] [Article]