Spatiotopic selectivity of adaptation-based compression of event duration

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A. Bruno, I. Ayhan, and A. Johnston (2010) have recently challenged our report of spatiotopic selectivity for adaptation of event time (D. Burr, A. Tozzi, & M. C. Morrone, 2007) and also our claim that retinotopic adaptation of event time depends on perceived speed. To assist the reader judge this issue, we present here a mass of data accumulated in our laboratories over the last few years, all confirming our original conclusions. We also point out that where Bruno et al. made experimental measurements (rather than relying on theoretical reasoning), they too find clearly significant spatiotopically tuned adaptation-based compression of event time but of lower magnitude to ours. We speculate on the reasons for the differences in magnitude.

Keywords: spatiotopic selectivity, adaptation-based compression, event duration

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Introduction

Several recent studies have shown that the perception of event time is strongly linked to space, in interesting ways. Morrone, Ross, and Burr (2005) first showed that perceived time is compressed during saccades to about half the physical duration and also when attention is diverted in a dual task (Cicchini & Morrone, 2009). With a different paradigm, Johnston, Arnold, and Nishida (2006) demonstrated that adapting a specific region of the visual field with a fast-moving grating selectively compresses the perceived duration of stimuli subsequently presented to the adapted region. Burr, Tozzi, and Morrone (2007) went on to show that the adaptation comprised two components, one "retinotopic," moving with the eyes, and another "spatiotopic," anchored in world-centered (or at least head-centered) coordinates. The retinotopically selective adaptation of time was strongly linked to speed perception: when the apparent speed in the adapted and non-adapted regions was matched, this effect disappeared. More recently, Morrone, Cicchini, and Burr (2010) showed that higher order adaptation is indeed spatiotopic (not merely craniotopic), remaining fixed in space with head turns.

In a recent issue of this journal, Bruno, Ayhan, and Johnston (2010) have challenged our results, both the existence of spatiotopic adaptation-based compression of event duration and that the retinotopic effects are related to the well-known effects of speed on perceived time. Since our initial publication, our laboratory has continued to study adaptation of duration, and we have now accumulated a reasonably large database on these effects, largely unpublished. To help readers arrive at an informed opinion on the important issues of event timing, and spatiotopicity in general, we believe it useful to lay out all these data, collected in different laboratories (in Milan, Pisa, Florence, and Perth) under the supervision of different chief investigators for different purposes. Full experimental details are given in the Methods section and Table 1.

It has long been known that adapting to fast motion causes subsequent inspection of moderate speed motion to

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Experiment	Bruno's Experiment 4	Bruno's Experiment 5	Bruno's Experiment 6	Burr et al. (2007)	Morrone et al. (2010)	Unpublished MC	Unpublished RA
Color code	–	–	–	Blue	Red	Green	Purple
Principle investigator				Burr	Cicchini	Cicchini	Arrighi
Contrast of adaptor	50%	50%	90%	90%	90%	85%	90%
Frequency of adaptor	20 Hz	20 Hz	20 Hz	20 Hz	20 Hz	20 Hz	20 Hz
Reversals of adaptor	every 250 ms	every 2 s	every 2 s	every 2 s	every 2 s	every 2 s	every 2 s
Initial adaptation	20 s	44 s	45 s	40 s	50 s	50 s	40 s
Top up	10 s	8 s	8 s	8 s	8 s	8 s	7 s
Contrast of test	100%	100%	90%	90%	85%	80%	90%
Adapted presented first	Yes	Yes	Yes/no/mixed	Yes	Yes	Yes	Yes
Size of saccade	10°	15°	13°	15°	12°	12°	15°
QUEST/constant stimuli	CS	CS	Q	Q	Q	Q	Q
Mixed/blocked	Mixed	Mixed	Blocked	Mixed	Blocked	Blocked	Blocked
Adapted duration range (ms)	600	600	600	600	600	600	150–1800
Unadapted duration range (ms)	300–1200	300–1200	150–1200	150–1200	150–1200	150–1200	600
Pauses between adaptation/test	800 ms	800 ms	800 ms	800 ms	1500 ms	1500 ms	1300 ms
Pauses between test/probe	500 ms	500 ms	500 ms	500 ms	1200 ms	1200 ms	500 ms
Retinotopic (unmatched)							
Averaged speed (test/probe)	10/10 Hz	10/10 Hz	10/10 Hz	10/10 Hz	10/10 Hz	10/10 Hz	–
Number of subjects	3 (1 naive)	4 (2 naive)	11/11/11 (8 naive)	8 (6 naive)	5 (4 naive)	4 (3 naive)	–
Mean effect (ms)	176	220	123/115/105	179	161	100	–
Mean effect (%)	29.4	36.6	ca. 20/19/18	29.8	26.8	16.7	–
P-value for one-tailed *t*-test	<0.003	0.015	all <0.01	<0.003	0.007	0.014	–
Retinotopic (matched)							
Averaged speed (test/probe)		–	–	10/7.1 Hz	16.5/10 Hz	18.2/10 Hz	18.5/10 Hz
Number of subjects		–	–	8 (6 naive)	7 (6 naive)	4 (3 naive)	8 (7 naive)
Mean effect (ms)		–	–	−14.3	18	24	34.7
Mean effect (%)		–	–	−2.4	3	4	5.78
P-value for one-tailed *t*-test		–	–	0.77	0.2	0.056	0.246
Craniotopic							
Averaged speed (test/probe)	10/10 Hz	10/10 Hz	10/10 Hz	10/9.3 Hz	11.1/10 Hz	11.7/10 Hz	12.5/10 Hz
Number of subjects	3 (1 naive)	4 (2 naive)	11/11/11 (8 naive)	8 (6 naive)	7 (6 naive)	5 (4 naive)	8 (7 naive)
Mean effect (ms)	−0.9 ms	39.4	ca. 45/40/37	157	101	74	140
Mean effect (%)	−0.15	6.5	ca. 7/7/6	26.1	16.8	12.3	23.3
P-value for one-tailed *t*-test	0.49	0.03	0.03/0.07/0.06	<0.003	0.003	0.01	0.04

Table 1. Experimental details for the various studies reported here. Other details in Methods section.

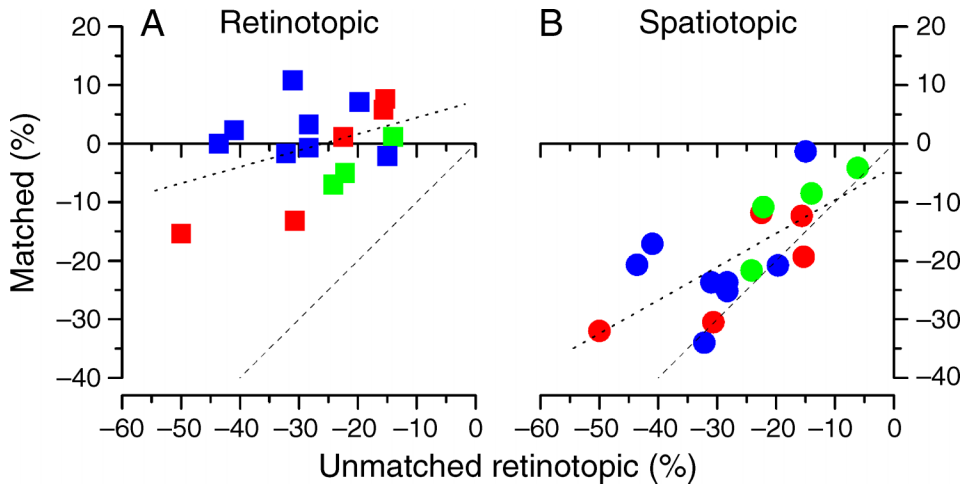

Figure 1. Retinotopic and spatiotopic adaptation-based compression of duration under conditions where either the perceived (ordinates) or physical speeds of the probe and test were matched. In all cases, the values reflect the percentage of reduction in apparent duration of a brief (600 ms) grating drifting at 10 Hz after adaptation to a 20-Hz grating. Psychophysical functions (minimum of 70 points per subject) were measured both before and after adaptation and reduction given by $(PSE_{adapt} - PSE_{no\text{-}adapt})/600 \times 100\%$. Subjects made a saccade after adaptation, which was followed immediately with the test stimulus presented either in the same retinotopic (relative to fixation) or spatiotopic (screen) location of the adaptor. The color coding refers to different experiments, with slightly different experimental conditions, described in the Methods section. The dashed lines are the equality lines, and the dotted lines are linear regression of the data.

appear slower (Thompson, 1982; Wohlgemuth, 1911), and it is also well known that apparent duration depends on speed (Kanai, Paffen, Hogendoorn, & Verstraten, 2006; Roelofs & Zeaman, 1951). However, Bruno et al. (2010, p. 3), noting that "the function relating perceived duration to temporal frequency saturates at around 4–8 Hz or 8 deg/sec (Johnston et al., 2006; Kanai et al., 2006; Kaneko & Murakami, 2009)" claim that "changes in apparent temporal frequency in the range tested should have little effect on perceived duration." It is always difficult to draw firm conclusions from experiments conducted under different conditions for different reasons. Kanai et al. (2006) did not use large peripheral gratings like ours and Bruno et al.'s but mainly small patches at fixation. Nevertheless, it should be understood that the effect of speed on time is huge, in the order of 300–400 ms, so even at the point that Kanai et al. define as saturation (67%), there is still 100 ms of compression left. Under the conditions least dissimilar to ours, moving random dots (their Experiment 2), duration varied monotonically with speed in the range of 8–16 deg/s, by about 80 ms over the range relevant to our experiments.

However, given the gross differences in stimuli and procedure, the prudent course is surely to measure time compression with both perceptually and physically matched stimuli. The basic procedure to measure retinotopic or spatiotopic adaptation-based time compression was for observers to adapt to a fast-moving grating (usually 20 Hz), then saccade to the other side of the adapting grating. Then, the test grating (usually a 10-Hz drifting grating presented for 600 ms) could be presented either in the same position as the adaptor on the screen (spatiotopic) or on the retina. The test was followed by a probe displayed in a neutral position (neither spatiotopic nor retinotopic). We made these measurements both in conditions where the test and probe speeds were matched individually for each subject, by increasing the test or decreasing the probe, and when they were physically equal. Figure 1A shows individual data for all subjects on which we have retinotopic adaptation (difference between adapted and unadapted duration PSE expressed as a percentage) for both matched stimulus and unmatched speeds, plotting the amount of duration compression in one condition against the other. Mean compressions, together with standard errors and standard deviations, are reported as bar graphs in Figure 3.

The first clear observation is that matching the speed of the probe grating to the perceived speed of the test has a major impact on estimates of perceived duration in the retinotopic condition. When the apparent speed was not matched, adaptation reduced perceived duration by an average of 26% (155 ms), more than twice the standard deviation of the distribution, and 9 times the standard error of our sample. On the other hand, when the probe was matched to the perceived speed of the test (either by increasing the physical speed of the test or decreasing that of the probe, depending on experiment), the mean change in duration was essentially zero. Although there was considerable variability in the data (standard deviations above 10%), there was no single observer who did not show an adaptation-based reduction in event duration, and all showed far less with speed-matched stimuli (all symbols well above the equality line). Figure 2A plots the percentage reduction in apparent duration as a function of the speed match for each subject. The diamonds refer to when the speed of the probe was reduced to that of

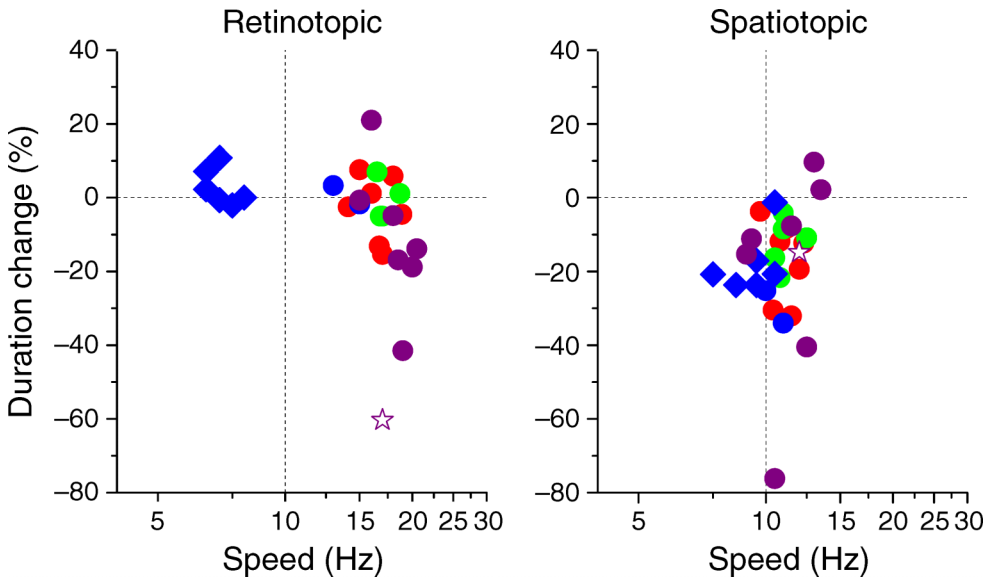

Figure 2. Retinotopic and spatiotopic adaptation-based compression of duration plotted against the matched speed of the probe (diamonds) or the test (circles). Like Figure 1, the color coding refers to different experiments, described in the Methods section. The star symbols show data for the subject under Fluoxetine medication, clearly anomalous, and not included in means or other analyses.

the test (all from Burr et al., 2007) and circles when the test speed was increased to match the probe. Note that the purple symbols (from "RA unpublished") refer to data not plotted in Figure 1, as there were no measurements taken without speed matching. These are, however, included in the means of Figure 3 (except the star symbol, discussed below).

The data for spatiotopic adaptation (Figure 1B) were quite different. For these too, the stimuli were matched in speed, but the match caused only minimal physical change (Figure 2B), as this form of adaptation has very little effect on the speed of stimuli in the same spatiotopic position (Burr et al., 2007; Wenderoth & Wiese, 2008). Our data show an average compression of 18%, 1.5 standard deviations below zero, clearly significant ($p < 0.0001$, $t = 7.5$, $df = 26$). Again, the effect held for most observers, although there was considerable scatter. Interestingly, there was a significant correlation between the spatiotopic effect and the retinotopic effect for unmatched speeds (slope = 0.56, $R^2 = 0.49$, $p = 0.001$), suggesting that some of the variance may reflect a real inter-subject difference. On the other hand, there was very little correlation between the matched and unmatched retinotopic results (slope = 0.28, $R^2 = 0.18$, $p = 0.1$), nor between the matched retinotopic and spatiotopic measurements ($R^2 = 0.03$, $p = 0.45$), suggesting that most of the variance in the matched retinotopic condition came from measurement error, or perhaps imperfect speed matching. Also consistent is the fact that there was less variance in this condition—$99\%^2$, compared with $(135\%)^2$ for unmatched retinotopic and $(153\%)^2$ for spatiotopic.

The individual data of Figures 1 and 2 are color-coded to show from which experiments they arise. It is clear on inspection[1] that the data of the original publication (color-coded blue) do not differ from those of the more recent experiments, run under slightly different conditions (described in the Supplementary material), in different laboratories on different monitors by different experimenters, with subtly different instruction sets for different subjects. So while there is clearly considerable variability

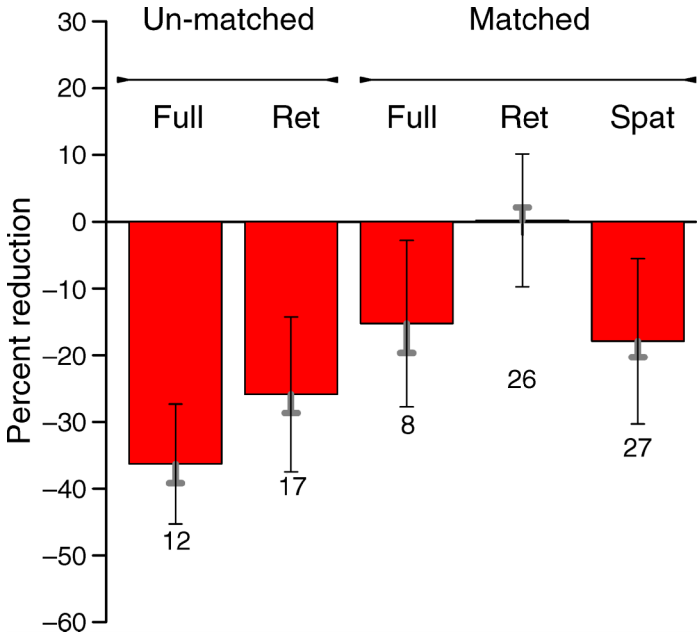

Figure 3. Average compression of interval duration (defined in Figure 1) under various conditions, with and without matching for speed. The short thick error bars show ±1 *SEM*, and the long thin ones show ±1 standard deviation. Numbers near the bars refer to the number of subjects in this condition.

in the data, the trend of results has been robust over time (and space).

So what could explain the differences between the results obtained in our laboratory and those of Bruno et al. (2010)? The effects of speed matching are perhaps the easiest to account for, as Bruno et al. did not actually measure this effect but relied only on very qualitative theoretical arguments. Our careful measurements on the 17 subjects of Figure 1 show a large and robust effect of speed matching, difficult to refute by theoretical cogitation. Although Bruno et al. did not make the obvious measurements with matched stimuli, they did devise an interesting double-adaptation technique (alternate adaptation to 5 and 20 Hz). Although this procedure left perceived speed unchanged, it led to retinotopic adaptation for the small subset of their population tested (three, including two authors). This is certainly an interesting result, meriting further investigation; but even if it does turn out to generalize to a wider range of subjects, it is hard to understand exactly what is going on, particular under their conditions of tracking the stimulus: saccades certainly affect time perception (Burr et al., 2007), and so do pursuit eye movements (Schutz & Morrone, 2010). Adaptation is poorly understood at the best of times, and double adaptation is likely to produce many complicated effects that are difficult to monitor. In their previous study, Johnston et al. (2006) explored the effects of speed matching and concluded that this could not explain their effects. We have no explanation for this discrepancy, but invite readers to observe these simple stimuli for themselves: successive 600-ms gratings, one drifting at 10 Hz, the other at 7 Hz (the apparent speed after adaptation). There is a clear difference in apparent duration, particularly when presented in the periphery (as our conditions require) the effect is large and obvious. On request, we will provide a demo program that operates in Psychtoolbox.

It is also difficult to explain why Bruno et al. find a smaller spatiotopic effect than ours, only 7% compared with our 18%. However, let us be clear. Despite their repeated claims throughout their manuscript that they find "no significant change in apparent duration following retinotopic adaptation" (Bruno et al., 2010, abstract), their spatiotopic adaptation results *are in the predicted direction and statistically significant*. Their Figure 6A (Experiment 6) reports the data for the largest group of subjects ($n = 11$). The spatiotopic effect for their "standard-first" condition (most similar to ours) is 7.3%, with standard errors around 3.6%. Student's t (given by the ratio of the mean to the standard error) is 2.03, which is significant (p(one-tailed) = 0.035, $df = 10$). Obviously, as the hypothesis being tested is compression (no one has ever suggested that adaptation to a fast-moving grating should lead to an expansion of time), the test must be *one-tailed*. The standard-first condition is the most relevant condition, as adaptation effects decay with time, but the "standard random" condition was also significant ($p = 0.047$, $t = 1.85$). Even in the "standard-second" condition, when the effects have had up to 2 s to decay, the effect was marginally significant ($p = 0.068$, $t = 1.62$). In addition, Experiment 5, also similar to ours, shows a significant effect ($p = 0.03$). So with two separate subject groups and three different paradigms, they show time compression of around 7%, about 2 standard errors from zero (see Table 1 for individual p-values). We would need original data to analyze the variance of all these data, but the probability of all four different conditions producing effects in the predicted direction with these p-values is clearly very low indeed. It would also be interesting if Bruno et al. were to reanalyze their data excluding the non-naive subjects, to see if they affected either the significance or the magnitude of the effects.

It is true that the significant effects reported by Bruno are weaker than those that we routinely obtain, for reasons we can only speculate on. One possibility is chance selection of a different subject pool. Possible, but unlikely from chance alone, as an unpaired t-test puts the probability of the two samples of results coming from the same population at less than 1% ($p = 0.008$, $t = 2.82$, $df = 36$). Presumably, some subtle differences in testing procedure weakened the effects in Bruno's laboratory. Adaptation effects are complex and may be expected to be even more complex if working simultaneously at several levels. For example, recent fMRI studies found that obtaining orientation-tuned adaptation signals in V1 requires long-term (several seconds) adaptation (Fang, Murray, Kersten, & He, 2005), whereas adaptation effects in extrastriate areas were seen after very short-term adaptation (Henson, 2003). Again, differences in duration seem unlikely, as the adaptation durations were reported to be the same in both experiments, but this should be noted as a potential confound. It is possibly also relevant that adaptation, particularly to motion, is strongly dependent on attention (Alais & Blake, 1999; Chaudhuri, 1990). Indeed, the spatiotopic selectivity for BOLD signals is also strongly dependent on attention (Crespi et al., 2009). Subjects in our studies (mostly students in advanced perception classes) participated willingly and were highly motivated to collect careful data (while ignorant of the goals of the study). They were trained for some time before collecting data and also instructed to pay attention to the stimuli. Our recording sessions were kept short so as not to tire or bore them. However, the total testing time of each subject was usually around 4–5 h, spread over several days.

We suspect that other factors also contributed to the weaker effects obtained in Bruno's laboratory. We note that in the first series of experiments (where no spatiotopicity was reported), the Michelson contrast of Bruno et al.'s study was 100%, whereas it was reduced to 90% for the second series, the one that showed significant spatiotopicity. On most monitors, linearity is difficult to maintain at 90%, even by the most rigorous researchers, and virtually impossible at 100%, often leading to abrupt changes in mean luminance when grating are turned on and off. We do not know how these abrupt changes in

luminance may affect apparent duration, but it would seem to be more prudent to keep contrast to the linear range.

Bruno et al. enter into a complex argument about temporal order effects. However, all the data reported here are calculated as the difference between adapted and unadapted conditions, so any temporal order effects should cancel out. Obviously, we chose to present the test stimulus (in the adapted location) first, before the effects of adaptation had worn off (and we do not know how quickly the various low- and high-level effects on duration decay). Bruno et al. also suggest that subjects may have been making judgments relative to a running average (as in the method of constant stimuli: Morgan, Watamaniuk, & McKee, 2000), rather than comparing the test with the probe. Several lines of evidence speak against this. As detailed in Table 1, some data were collected in blocked trials (spatiotopic and retinotopic conditions separately), others with retinotopic conditions intermingled with spatiotopic conditions. These lead to a different running average (as the retinotopic condition had no effect on duration in our hands), yet the results did not differ. Finally, in most studies, we adjusted the duration of the probe stimulus, leaving the test constant at 600 ms, so the perceived duration of both test and probe varied considerably with the adaptation condition. In one later study (RA unpublished), we increased the test rather than decrease the probe, so the perceived duration hovered around 600 ms. Again, both types of procedures produced very similar results.

The star symbol in Figure 2A reports data of one subject who is clearly an outlier, showing very large levels of retinotopic-based adaptation in the speed-matched condition (s/he was not tested in the unmatched condition). This subject revealed on interview to be under Fluoxetine medication (20 mg/day for 1 year) and therefore not included in the averages or statistical analyses. We certainly do not wish to draw any strong general conclusions from one single subject, but this highly anomalous result underlines the delicacy of these measurements. Fluoxetine is known to have profound effects on the visual plasticity of the adult brain (Maya Vetencourt et al., 2008). There are no previous reports of the effects of Fluoxetine on time perception, but it is known that time perception can be altered radically by various pharmaceuticals, such as amphetamines (e.g., Cevik, 2003; McClure, Saulsgiver, & Wynne, 2009; Meck, 1996). We are certainly not suggesting that Bruno et al. were under the influence of pharmaceuticals, but the data of this single subject does highlight how delicate adaptation studies on time can be.

Bruno et al. (2010, p. 2) claim that "we challenge their interpretation that the adaptation effects occur at an early site." Not so. While our clear evidence for spatiotopic adaptation suggests involvement of higher, spatiotopically tuned neural centers, this in no way excludes the involvement of lower levels of analysis. Electrophysiological studies suggest that adaptation occurs at all levels: the presence of adaptation at one level cannot be taken as evidence for its absence at another level. Indeed, we believe our speed-matching technique allows us to separate out two levels of adaptation effects: one, presumably early level, that affects both speed and retinotopic adaptation; and another, presumably higher level, that has minimal effects on speed but adapts the perceived duration of objects in that position in external space. One candidate mechanism for this adaptation has been reported by Mayo and Sommers (2010): performance of macaque monkeys in a duration task is best predicted by the *amplitude* rather than the *latency* of responses in prefrontal cortex and deep layers of the superior colliculus. Adaptation of these areas could lead to responses of lower amplitudes, in turn leading to encoding of briefer times. Saccades could have similar effects, also causing compression of time (Morrone et al., 2005).

Bruno et al. (2010) also report that adaptation-based duration effects do not transfer between eyes. In our original paper, we tested only 3 subjects dichoptically and have since added only one extra subject (author GMC), who also shows the effect (21% dichoptic time compression for full adaptation, 11% spatiotopic). However, as the subject pool still remains low, we are less confident that this effect can be generalized to the entire population and are happy to leave it as an open issue.

Most readers of this journal are familiar with psychophysical studies such as contrast sensitivity or acuity or similar, where there is very little inter-subject difference. Clearly, under those circumstances, it is sufficient to measure carefully two or three subjects, usually the authors. The effects reported here almost certainly reflect higher level processes, and these seem to show both more variability between subjects and less robustness to changes in conditions. This necessarily implies a different approach. Rather than just two or three trained and trusted subjects we need a much wider range, including subjects unaware of the experimental goal, but at the same time, it is imperative that data collection be performed with considerable care, under conditions where subjects pay full attention to the task, where sufficient data are collected to produce reliable psychometric functions, where experimental conditions (such as calibration of monitors) are rigorously controlled, and that clear anomalies in subjects, such as medication, are controlled for.

Understanding spatiotopicity is important, one of the major keys to understanding how space is represented in the brain. Whereas retinotopy is, at least in principle, easy to explain, in that it reflects the topographic retino-cortical connections, spatiotopicity is a more complex and subtle phenomenon. Despite the enormous research effort aimed at revealing mechanisms implicated in spatiotopicity, such as shifting receptive fields (Duhamel, Colby, & Goldberg, 1992), the identification of the pathways for the corollary discharge (Sommer & Wurtz, 2002, 2006), and neurophysiological evidence for true spatiotopicity in both monkey and human (e.g., Crespi et al., 2009; d'Avossa et al., 2007; Duhamel, Bremmer, BenHamed, & Graf,

1997; Goossens, Dukelow, Menon, Vilis, & van den Berg, 2006), we are still far from a complete explanation of how spatiotopicity comes about. Understanding the mechanisms responsible for the perceptual experience of stability in the face of continued eye movements will be one of the more exciting challenges of the next few decades, a challenge that needs to be met with careful and rigorous research, free from prejudice and preconception.

Methods

The main parameters of Bruno et al.'s studies most similar to ours, and our own, are given in Table 1. All of these experiments followed a similar basic paradigm: each session started with an initial adaptation phase (duration given in table) followed by the presentation two stimuli, one in the adapted region ("standard" for Bruno et al., "test" for us), the other in a non-adapted region ("comparison" for Bruno et al., "probe" for us). Subjects were required to report in forced choice which interval appeared longer. Before each trial, there was a "top-up" adaptation period (duration in table). In most studies, the standard/test was of fixed duration, always 600 ms, while the probe varied. In the RA unpublished study, the probe stimulus (in the neutral region) was fixed and the adapted stimulus is varied in duration. In all our studies, duration of variable stimulus (usually probe, test for "RA unpublished) was determined by the adaptive QUEST algorithm (Watson & Pelli, 1983). In the first session of each condition (usually 30 trials), the algorithm started at 600 ms (matched physical duration), then estimated PSE after each trial. The value for the next trials was the running estimate of PSE, added to a random number (drawn from a Gaussian distribution of mean zero and standard deviation 30 ms). This procedure ensured that there was considerable scatter around the PSE, and that the number of "greater than" and "less than" trials were roughly equal. Subsequent sessions started with the estimate of PSE from previous sessions in that condition. Usually 3–5 sessions were run for each condition, in randomized order. The final estimate of PSE was taken as the median of the best-fitting cumulative Gaussian function to all the data of a particular condition (percentage "greater than" against duration).

A total of 26 subjects participated in this study, almost all naive to the goals at the time of testing. Subject RA participated in 2 studies (Burr et al.—as a naive—and "RA unpublished") and GMC served as subject in Morrone et al. (2010) as well as in "GMC unpublished." Thus, we have 28 data points for the most tested condition (speed-matched spatiotopic). One subject was excluded when found to be on medication, leaving 27 data points for this condition: 22 from observers naive at the time from 25 different people. The average in the retinotopic condition was calculated from 26 data points, because one subject dropped out of the study.

The studies of craniotopic or spatiotopic effects used an adaptor above or below midline (except for RA unpublished where the adaptor was displayed on the midline). After adaptation, subjects made a saccade (usually rightward but sometimes leftward) to the other side of the adaptation stimulus, after which the test was presented either in the same screen location as the adaptor (spatiotopic condition) or was in the same position relative to fixation (retinotopic condition). Usually the test (or reference) stimulus was presented first in the sequence to test adaptation while it was strongest (except Bruno et al.'s Experiment 6: see table).

Most of our studies used stimuli that were matched either in physical or apparent speed. The apparent speed match was achieved in one of two ways: either the test (adapted) stimulus was increased in speed to match that of the non-adapted probe or the probe was decreased to match the adapted test (details in table and Figure 2). In all cases, a QUEST procedure was used to determine the speed of the test or the probe, homing in on the speed match. PSE was given as the mean of the psychometric functions, with a minimum of 70 data points. In the spatiotopic condition, speed needed to be varied little in practice, by about 15%. For the retinotopic condition, speed was varied by 66% on average. The averages for each experiment are given in Table 1 and the individual values in Figure 2.

Most stimuli were black and white gratings on a gray background, except "RA unpublished study," designed to test "objectopy," where the stimuli were black and white but the background was bright yellow (CIE x, y, Y: 0.328, 0.381, 59.5 cd/m^2). In this paradigm, each trial started with subjects fixating a red spot presented on the horizontal midline 7.5 deg left of screen center. After 500 ms, the adaptation phase begun with a patch presented centrally in the screen along the horizontal midline (see table for other details). At the end of the adaptation period, the adaptor was replaced with a gray circle of matched luminance (59 cd/m^2), and subjects saccaded to a point 15 degrees to the right (across the gray circle). After 300 ms from the appearance of the new fixation point, the gray oval started to rotate steadily in a circular trajectory of around 7.5° radius around fixation point lasting 1 s, to one of three randomly chosen angles: 0° (the same spatial location of the adaptor), 90°, or 180° (same retinotopic location of adaptor). Three hundred milliseconds after the animation ceased, the gray patch transformed into a drifting grating of variable duration (the test), followed by a fixed duration probe stimulus 7.5° below fixation.

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Footnote

[1]Unpaired two-tailed Student's *t*-tests between the original and all later data, separately for the various conditions, failed to show any significant effects.

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