Retinotopic selectivity of adaptation-based compression of event duration: Reply to Burr, Cicchini, Arrighi, and Morrone

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There are two points at issue here. The first is whether there is a robust adaptation-based duration compression in a spatiotopic frame of reference (when the eye moves and the stimulus is placed in the same screen position as the adaptor). The second is whether there is perceived duration compression in a retinotopic frame of reference (when the eye moves and the stimulus is placed in the same retinal position).

The first issue is the robustness of the spatiotopic effect reported by Burr, Tozzi, and Morrone (2007). We reported a trend in the spatiotopic direction when the standard was presented first but not when the standard was presented second (Bruno, Ayhan, & Johnston, 2010). We used a two-tailed test because for a one-tailed test it would have been necessary to ignore a significant difference in the direction opposite to the expectation. We have previously found expansion after adaptation in regions surrounding the test (Ayhan, Bruno, Nishida, & Johnston, 2009) and after 5-Hz adaptation in dyslexics (Johnston et al., 2008), therefore apparent duration expansion is possible, and if we found expansion, we would want to report it. We should also report that the number of subjects was set before the start of the experiment, there were no outliers, and no subjects were removed from the analysis.

Burr et al. (this issue) invited us to report the results of Experiment 6 (Bruno et al., 2010) for the spatiotopic conditions with the authors removed. We used a bootstrapped one-sample *t*-test (PASW) given the smaller *N*. With the authors, the *p*-values are Standard First $p = 0.072$, Standard Second $p = 0.172$, and Standard Random $p = 0.108$. Without the authors, we have Standard First $p = 0.097$, Standard Second $p = 0.223$, and Standard Random $p = 0.034$. With Bonferroni correction (criterion 0.016 for 3 tests), the trend, reported in our paper in the spatiotopic conditions, just fails to reach significance, with or without the three practiced observers. We do not deny the possibility of finding a significant spatiotopic effect using Burr's laboratory paradigm; they indeed have reported such effects; however, in our study, the trend we saw in that direction did not reach significance on a two-tailed test and did not occur robustly in all conditions.

We do not see a spatiotopic trend in trials in which the standard (in the adapted region) is presented second. Presenting the standard second introduces a delay between switching off the adaptor and switching on the standard of an additional 700–1500 ms. Burr et al. attribute this to a decay of the spatiotopic effect within this period. We attribute the difference to a switch in strategy in the standard first adaptation trials with observers choosing to ignore the standard and simply comparing duration on any given trial relative to the mean of the set. Burr et al. point out that in some of their experiments trials were mixed and in other trials were blocked, so subjects could not use a running average of stimuli as a standard. However, Morgan (1992) has shown that subjects can have the same discrimination thresholds for multiple standards in interleaved versions of the method of single stimuli as when trials are blocked.

The lack of a spatiotopic effect in our Experiment 4 is considered by Burr et al. to be due to possible artifacts in the stimulus resulting from the use of 100% contrast test patterns rather than 90%. We calibrated our monitor using the ColorCal and the standard software and procedure for the Cambridge Research Systems Visage. Even if higher spatiotemporal harmonics exist in our stimulus, it is not clear why these would have masked spatiotopic adaptation. We also find full adaptation-based duration compression using balanced high- and low-frequency adaptors and low-contrast test patterns (Ayhan et al., unpublished data) and for invisible adaptors (Johnston et al., 2008).

Of concern to us is Burr et al.'s (2007) claim that purely retinotopic effects are mediated by changes in apparent temporal frequency and there are no direct effects of temporal frequency adaptation on perceived duration. Burr et al. (2007) following Johnston, Arnold, and Nishida (2006) used temporal frequency matching. Since perceived duration can be influenced by temporal frequency, this requires an accurate match. In the original paper, Burr et al. reduced the temporal frequency of the comparison, as we had done previously, to match the adapted standard. Note that temporal frequency discrimination (Weber fraction) sharply declines above 7 Hz and is poorest around 20 Hz, rising again for high frequencies (Mandler, 1984). In much of the data presented in their response to our paper, they null the reduction in temporal frequency in the adapted region after adaptation to 20-Hz drift by increasing the temporal frequency of the adapted standard from 10 Hz to, on average, 17.5 Hz and in at least in one case to 21 Hz (Figure 2A of Burr et al.). Matching in this way introduces a large physical difference between the standard and comparison and leads to high temporal frequency samples in the psychometric function.

A high temporal frequency in the adapted region might be expected to work against any perceived compression to the degree to which high temporal frequencies appear expanded. However, subjects with a high temporal frequency standard (>17.5) tend to see this interval as compressed (Figure 2A of Burr et al.). You might like to try this condition for yourself. Adapt to a 20-Hz drifting stimulus then switch gaze and compare the duration of a 600-ms 17.5-Hz stimulus in the adapted region against a 600-ms 10-Hz stimulus in an unadapted region (code available on application). If you see temporal compression, as we do, this indicates that retinotopic compression can occur in a situation where the apparent temporal frequency is matched (by Burr et al.'s method) and the physical temporal frequency is high.

However, there is a better way to dissociate changes in duration and temporal frequency. Bruno et al. (2010) adopted a procedure used by Ayhan et al. (2009) to eliminate changes in apparent temporal frequency. The effects of adapting to 5-Hz and 20-Hz drifts on apparent temporal frequency perception are in the opposite direction (Johnston et al., 2006), so canceling, whereas the effects of adapting to 5-Hz and 20-Hz drifts on the apparent duration of the standard (10 Hz) are in the same direction. This fundamental dissociation undermined the proposal that changes in apparent duration are simply mediated by changes in apparent temporal frequency. See Johnston (2010) for a further discussion of this. By mixing high- and low-frequency adaptors, we can keep the test patterns physically and perceptually the same in terms of temporal frequency while measuring apparent duration. This method is preferable to matching as it avoids any intrinsic difference between the standard and comparison, which might affect the perceived onset or offset of the interval or the perceived duration of the interval. To isolate retinotopic adaptation, we moved the adaptor with the eye so that we did not differentially adapt any particular region of space. Note that though eye movements can affect time perception (Burr et al., this issue), the pursuit eye movements during adaptation precede both standard and comparison stimuli.

Perhaps paradoxically, it is the difference of opinion on how to explain the full adaptation condition that most clearly differentiates the two groups. Both groups agree on the facts. There is adaptation-based compression for a fixed eye, 20-Hz adaptation, a 10-Hz standard, and a comparison matched in temporal frequency to the apparent temporal frequency of the standard. Although Burr et al. (this issue) state adaptation can occur at multiple levels, Cicchini and Morrone (2009) say explicitly that "A subsequent study from our group (Burr et al., 2007) indicated that the alteration… (*referring to our duration compression result*)… is not related to an adaptation of the early analysis of the visual system but occurs only when the adaptor and the event to be timed occupy the same position in space, not on the retina." Their claim that there is no retinotopic adaptation for the *temporal frequency matched* stimuli implies that the full adaptation effect for matched stimuli must be due to spatiotopic adaptation. Since we find adaptation-based compression for a stimulus yoked to a moving eye, we attribute the affect to retinotopic adaptation.

Spatiotopic adaptation has been taken as evidence for the remapping of features to the expected location of these features resulting in a change of gain at those locations that will speed stimulus processing after the saccade (Melcher, 2005). As we point out in our paper, our participants are adapted to temporal frequency (Bruno et al., 2010). However, Burr et al. report that temporal frequency does not show spatiotopic adaptation, so there is no remapping of temporal frequency, which could affect processing in the stimulus region after the saccade. We did not have our participants adapt to higher duration intervals so there is no possibility of the remapping of duration as a feature in a putative duration channel (Aaen-Stockdale, Hotchkiss, Heron, & Whitaker, 2010). In addition, in the full adaptation condition, there is no eye movement, so there is no basis for the remapping of features or even shifts in pointers (Cavanagh, Hunt, Afraz, & Rolfs, 2010).

Burr et al. have yet to explain what mechanism would deliver spatiotopic adaptation-based duration compression without retinotopic adaptation-based duration compression. Spatiotopy could result from the gating of inputs to a single cell from across the whole visual field. This is the type of model that would gain support from spatiotopic adaptation effects (Cavanagh et al., 2010), since the same cell would receive input from two locations in the visual field. The problem with this model is that it requires each spatiotopic cell to get input from throughout the visual field and it is not clear how this could be achieved. It would also predict retinotopic adaptation.

Of course we agree with Burr et al. that progress in this area will require careful and rigorous research, free from prejudice and preconception. However, for a theory to become accepted, in addition to repetition, we also need generalization and triangulation. Converging evidence for spatiotopy in duration perception will need to come from other psychophysical paradigms and neurophysiological research. We think our pursuit-yoked adaptation experiment provides clear evidence for retinotopic duration compression.

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