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Neural mechanisms for timing visual events are spatially selective in real-world coordinates

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It is generally assumed that perceptual events are timed by a centralized supramodal clock. This study challenges this notion in humans by providing clear evidence that visual events of subsecond duration are timed by visual neural mechanisms with spatially circumscribed receptive fields, localized in real-world, rather than retinal, coordinates.

Accurate timing over the subsecond scale is essential for a range of human perceptual and motor activities, but the mechanisms for encoding this time scale remain poorly understood. Current research is beginning to call into question traditional ideas that events are timed by a centralized supramodal clock, in favor of distributed, modality-specific mechanisms[1]. Two recent studies from visual psychophysics are particularly challenging for centralized event timing: local adaptation of the visual field by fast-moving stimuli selectively reduces the apparent duration for stimuli presented to that position[2], and saccadic eye-movements drastically decrease the apparent duration of visual but not auditory events[3]. Although these results speak against a centralized supramodal clock, it remains unclear whether visual event timers show a genuine spatial tuning in external space, which would implicate high-level sensory mechanisms. In this study, we provide evidence that the neural mechanisms that time visual events are spatially selective in real-world coordinates, allowing them to separately time real objects localized in space.

Observers adapted to a grating drifting within a 12° diameter patch while fixating on a clear black spot to its lower left. After a suitable adaptation period, they made a saccade to a target that appeared 15° right of fixation (see **Fig. 1a** and ref. 4). Eight hundred ms after the display of the target, a test grating was presented for 600 ms in one of three randomly chosen positions: the same retinotopic position, the same spatiotopic position or in one that was neither (control condition). In separate sessions, subjects maintained fixation after adaptation, and the test was presented in the same (retinotopic and spatiotopic) position as the adaptor (full adaptation condition). Five hundred ms after the offset of the test, a probe grating of variable duration was presented at a fourth position, and observers indicated whether it appeared to be of shorter or longer duration than the test. The point of subjective equality (PSE) of the test and probe duration was estimated from the median of the best fitting cumulative Gaussian psychometric function (**Fig. 1b**).

As adaptation to high speeds is known to decrease apparent speed[5], and the apparent duration of moving stimuli depends on speed[6], we first matched the apparent speed of the probe to that of the test (separately for all subjects and conditions using standard staircase techniques), then used this speed-matched probe for subsequent measurement of perceived duration. For two subjects (triangles in **Fig. 1c**), we matched speed by increasing the speed of the test and leaving the probe at 10 Hz (although this had the disadvantage of lowering the apparent contrast of the test, a problem avoided with the other technique). In practice, speed-matching affected mainly the full and retinotopic adaptation conditions, with little change being necessary for the spatiotopic condition in six out of eight subjects. We then estimated the PSE of the test stimulus duration for the four adaptation conditions (results for representative naïve observer RA, **Fig. 1b**). Under all conditions, the psychometric functions rose smoothly from 0 to 1, with an s.d. around 80 ms. PSEs for both the control and the retinotopic adaptation conditions were near 600 ms, the actual duration of the test. Full adaptation reduced the PSE to 526 ms and spatiotopic adaptation to 456 ms. We plotted the percentage reduction in perceived duration (relative to control) for spatiotopic and retinotopic adaptation against that for full adaptation (results for all subjects, **Fig. 1c**). There was some variability in the magnitude of the effect, particularly for the full adaptation condition, but all eight subjects showed strong reduction in the spatiotopic condition and virtually none in the retinotopic condition. The average PSEs (**Fig. 2**) confirm this: retinotopic adaptation had little effect, with an average PSE of 591 ± 7 ms (near the control value of 600 ms), whereas the PSE for full adaptation was 476 ± 31 ms and 443 ± 22 ms for spatiotopic adaptation.

We also measured the apparent duration with the probe moving at the same physical speed as the 10-Hz test (**Fig. 2**). Under these conditions, the effect was strong for retinotopic adaptation (33%) and strongest for full adaptation (41%). Notably, the spatiotopic effect was virtually identical to the speed-matched condition (27% reduction), which was to be expected as the conditions were very similar, but shows that the effect does not depend on speed matching. The average PSEs for control runs with no adaptation had no substantial differences, confirming that the results cannot be attributed to spatial position, temporal order or the saccades themselves.

Finally we measured the effect dichoptically for three of the subjects, adapting the right eye and testing with the left (using ferroelectric goggles; **Figs. 1c** and **2**). Although the test and probes had identical speed in this case, there was very little retinotopic adaptation (bootstrap *t*-test, $P = 0.39$, not significant), whereas the spatiotopic adaptation was similar to the full adaptation, both significantly different from the control ($P = 0.001$ and $P = 0.002$, respectively).

These results suggest that at least two mechanisms are involved in adaptation of duration, one retinotopic and the other spatiotopic. The

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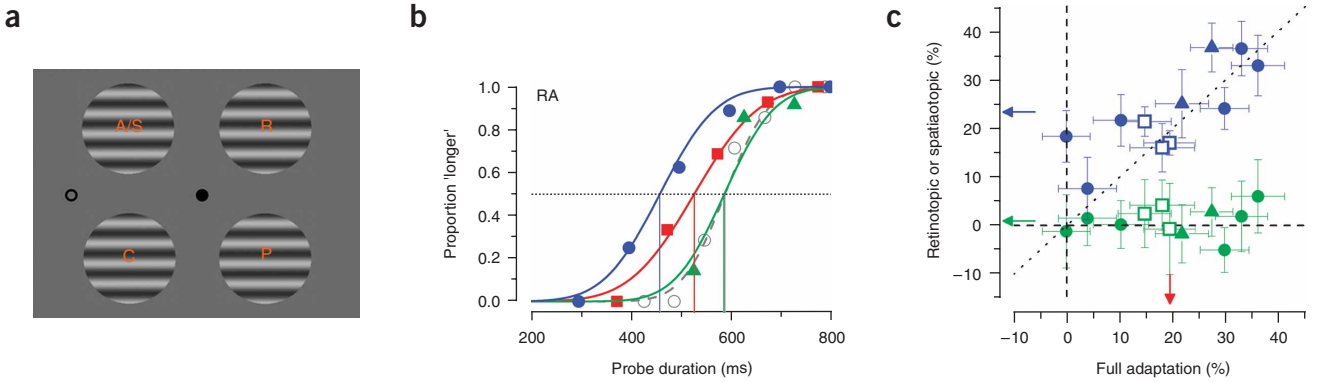

Figure 1 Illustration of stimuli and the effect of adaptation on perceived duration. (**a**) Illustration of stimulus condition. Eight observers (authors and five naïve) fixated on the point at left while adapting to a 1 c deg^{-1} horizontal grating drifting at 20 Hz (inverting direction every 2 s) within a 12° diameter patch centered 8° away in position A. After adaptation (initially 45 s with 8-s top-up between trials), the fixation point moved 15° rightwards, and observers saccaded to it within 200 ms. Eight hundred ms later, the test grating (1 c deg^{-1}, 10 Hz upwards or downwards) appeared for 600 ms, in one of the three randomly selected positions indicated S (spatiotopic), R (retinotopic) or C (control), all intermingled within a session. After a further 500 ms, the probe grating (also 1 c deg^{-1}) appeared at position P for a variable interval, and observers indicated whether its duration seemed shorter or longer than that of the test. Probe duration on each trial was drawn from a random Gaussian duration ($\sigma = 150$ ms) centered on a running estimate of PSE. In separate sessions, observers maintained fixation after adaptation with the test presented either to position S (spatiotopic and retinotopic) or position C (control). (**b**) Example psychometric curves for naïve observer RA for the control condition (gray open circles) and for full (red squares), retinotopic (green triangles) and spatiotopic (blue filled circles) adaptation, measured with probe matched to the apparent speed of the test (Average across subjects: full 5.2 ± 0.8 Hz, retinotopic 7.1 ± 0.7 Hz, spatiotopic 9.3 ± 1.2 Hz). The vertical lines indicate the PSEs of the four different conditions. (**c**) Effect of adaptation on apparent duration for the eight observers, calculated as the percentage reduction in the adapted condition compared with the control. The reduction for retinotopic (green symbols) and spatiotopic (blue symbols) adaptation is plotted against full adaptation, with color-coded arrows near the axes showing the averages. For two subjects (triangles) the test speed was increased to match the probe rather than vice-versa, to 14 Hz for retinotopic, 10.5 Hz for spatiotopic and 15 Hz for full. For these subjects, the stimuli positions were also inverted, with adaptation in the lower right field, saccades from right to left, and all other positions adjusted symmetrically. The open squares refer to dichoptic adaptation, with test and probe speed identical (10 Hz). Error bars show ± 1 s.e.m. calculated by bootstrap. The vertical and horizontal dashed lines show zero effect on duration, the diagonal shows equal effects.

apparent duration of visual stimuli increases with increasing speed[6], and adaptation to fast stimuli decreases the apparent speed of subsequently viewed stimuli[5]. Thus the retinotopically selective decrease in apparent duration, which occurred only when the tests and probe were not matched (so the probe seemed to drift much faster than the test), is probably an indirect consequence of the adaptor causing a reduction in the neural representation of speed, rather than of a direct action on neural timing mechanisms. Spatiotopic adaptation, however, occurred for both the speed-matched probes (which in practice changed little) and the 10-Hz probes, suggesting that its effects do not depend on changes in apparent speed (which are probably mediated by lower-level mechanisms), but reflect a direct action on the neural mechanisms of interval judgment. That dichotic adaptation was spatiotopically but not retinotopically selective also suggests that the spatiotopic adaptation occurs at a higher level than the retinotopic adaptation, as there is no anatomical convergence of eye input before V1, with strong functional interactions occurring only at later stages[7].

In the macaque, early visual areas including primary and secondary visual cortex have strong retinotopy that is unaffected by eye position, whereas some higher-order areas of parietal cortex seem to encode position in spatiotopic rather than retinotopic coordinates[8,9]. The lateral intraparietal cortical area, whose receptive fields are strongly affected by saccades[10], has been shown to be involved with the event timing of subsecond intervals[11], making it a plausible candidate for the spatiotopic-specific adaptation of duration. Transcranial magnetic stimulation studies[12] have also implicated this area in duration judgment in humans. Spatiotopic selectivity has not been studied extensively in humans, but recent functional magnetic resonance imaging results suggest that the portion of hMT+ that was thought to be retinotopic is in fact spatiotopic[13], and this could well be true of other parietal areas. All of these data fit well with our present results, suggesting that the spatiotopically selective neural mechanisms implicated in visual event timing probably reside in parietal cortex. This suggestion is reinforced by the gross and bizarre distortions of event-time that occur during saccades[3], the moment when spatiotopic maps are dynamically updated.

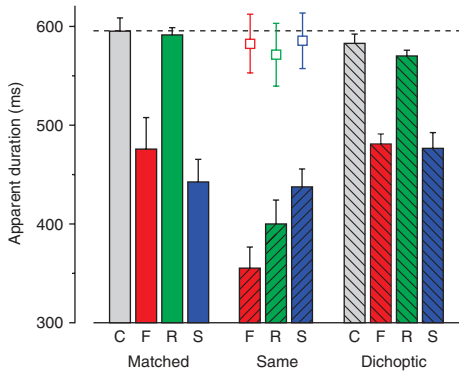

Figure 2 Average perceived duration for the control and three adaptation conditions (color-coded as for **Fig. 1b**). The plain bars at left refer to measurements with the probe drifting at the same apparent speed as the test ($n = 8$), the forward-hatched bars at center to the probe drifting at the same physical speed as the test ($n = 8$) and the backward-hatched bars to the dichoptic condition ($n = 3$). The upper square symbols show the mean durations measured in identical (binocular) conditions without adaptation. Average durations after adaptation were all significantly shorter than the control (separate one-tailed paired *t*-tests $P < 0.003$), except for speed-matched retinotopic adaptation ($P = 0.77$) and dichoptic retinotopic adaptation ($P = 0.30$). Error bars show 1 s.e.m.

Whatever the underlying physiological substrate, the results of this study clearly confirm the existence of spatiotopic neural mechanisms in humans (for which there has been little evidence to date[4,13]) and substantiate the intrinsic interconnection of space and time. These results also show that visual events are timed not by a centralized clock, but by neural mechanisms that are spatially selective (in real-world, not retinal coordinates). One recently suggested possibility[14] is that the cortical networks of neurons are inherently able to tell time as a result of time-dependent changes in network state. If these neurons were spatially tuned and adaptable, then stimulation with high temporal frequencies may slow down the dynamics of the network, leading to an underestimation of event duration.

Of course this leaves open the question of whether spatially localized timers can be monitored simultaneously. (Recent evidence[15] suggests that they cannot.) However, mechanisms of this sort could be the basis of timing specific perceptual events seen to occur in specific spatial positions: when watching a field of fireflies, we have a very clear idea of both the duration and the spatial position of any given flash, and this does not change if we make saccades. As humans saccade on average three times per second, it is certainly advantageous that the spatial selectivity of interval-timing mechanisms is grounded in external, rather than retinal, coordinates.

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COMPETING INTERESTS STATEMENT

The authors declare no competing financial interests.

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