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Visuomotor timing compensates for changes in perceptual latency

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The dimmer a stimulus is, the more time it takes the neural signal from the retina to reach visual cortex [1]. Presumably because of this variation in latency, a dim moving object appears to lag behind where it would appear if it were bright [2,3]. To investigate whether this flaw in perception afflicts our ability to interact with moving objects, we asked subjects to press a button at the moment a rotating bar became aligned with a stationary reference: over a 15-fold range of luminance, they did not respond later when the moving bar was dimmer. This suggests the visuomotor system compensates for changes in visual latency due to luminance variation, despite uncorrected lags in conscious perception.

To successfully interact with the environment, we must move our limbs at specific moments relative to external events. To do so accurately, we must compensate for the neural delays between sensory stimulation and cognitive processing, and between executive commands and muscle contraction [4]. It is not known, however, whether visuomotor timing corrects for the *variation* in neural latencies resulting from the large differences in light levels encountered in the natural environment.

Eight subjects fixated the center of a rotating bar and attempted to synchronize a button-press with the moment it became aligned with two stationary reference bars (Figure 1A). No feedback was provided. The luminance of the reference bars was 4.6 cd/m^2, and the moving bar's luminance varied randomly across trials from 0.3 to 120 cd/m^2, a range spanning photopic (cone-based, daytime) vision to the nighttime levels of mesopic (significantly rod-influenced) vision [5]. See the supplemental section online for detailed methods and results.

Across all luminance values, subjects tended to press the button before alignment, a typical finding with synchronization tasks [6]. As luminance dropped, responses did not become any later, contrary to the prediction based on neural latencies in the visual system [1]. Instead responses were unaffected or became slightly earlier (circular symbols in Figure 1B–D). This continued until the time of responses abruptly increased at the dimmest luminance tested (0.3 cd/m^2), a value near the rod-dominated regime. At least within a broad daylight range, therefore, visuomotor timing does not follow the luminance-based changes in sensory neural latencies.

Previous work, however, found that the conscious perception of moving objects *is* delayed by decreases in luminance [2,3,7]. In the Hess effect, the dimmer of two physically aligned moving objects appears to lag behind the brighter [2]. The flash-lag effect has a similar dependence on luminance: as a moving object gets brighter, it appears further and further ahead of an aligned stationary flash [3]. In two additional experiments, we confirmed these effects of luminance on perceived position under the stimulus conditions used in the synchronization experiment.

In our Hess effect experiment, the two reference bars were present throughout the trial and rotated at the same angular speed as the inner bar (Figure 1A). In the flash-lag experiment, the reference bars were flashed for 8 msec. In both experiments, the angle

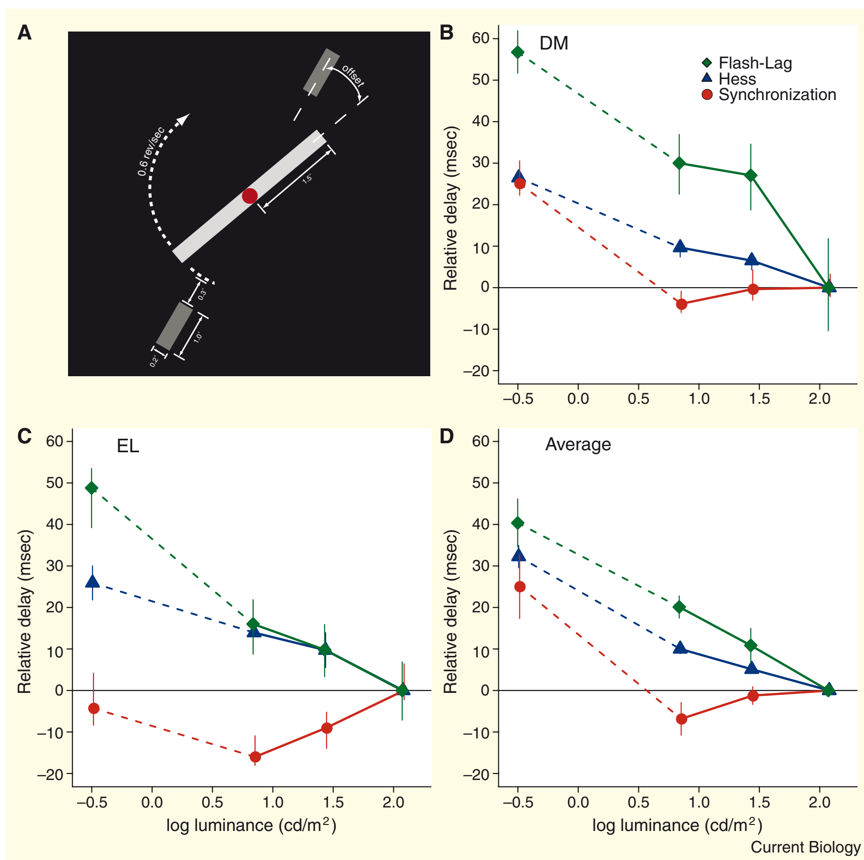

Figure 1. The stimulus display and results.

(A) The display used in all experiments, presented on a 120 Hz CRT. The sensorimotor synchronization task was to press a button at the moment the rotating inner bar became aligned with the stationary outer reference bars. In the flash-lag and Hess experiments, the task was to report whether the inner bar appeared ahead or behind the outer bars, which were positioned at a variable angle of offset relative to the inner bar, and were briefly flashed (in the flash-lag) or rotated along with the inner bar (in the Hess experiment). (B–D) Results plotted as the delays in perceived positions and button-presses relative to the brightest point. Different effects of luminance were seen for visuomotor synchronization and the other tasks, until the dimmest mesopic point (shaded region, connected by dotted lines) was reached. (B,C) Data for two naïve subjects. Error bars indicate the bootstrapped confidence interval (68.2%) that approximates one standard error. (D) The average data for eight subjects, of whom two did not participate in the flash-lag experiment. Error bars indicate ±1 standard error.

of offset between the inner bar and the references varied across trials and subjects reported whether the inner bar appeared to be ahead or behind of the references. The responses indicated that the dimmer the inner bar, the less far ahead it appeared to be (Figure 1B–D). To compare the effects of luminance in the three experiments, we fit lines to the plots relating log luminance to perceptual delays in the Hess and flash-lag experiments and to median temporal errors in the synchronization task. Bootstrapping [8] was used to test whether slopes were significantly different.

Within the photopic range (7–120 cd/m^2), the flash-lag slope (mean = 16.3 msec per log luminance) was significantly greater than the synchronization slope (mean = –5.5) for five of the six subjects ($p < 0.05$). The Hess effect slope (mean = 8.1) was greater for seven of eight subjects, and significantly so for five of them. These differential effects of luminance suggest that the mechanism triggering the button-press does not depend only, if at all, on the representation of the moving object that is consciously perceived.

Speeded reactions to unpredictable events are at least as delayed by decreasing luminance as the perceived positions in our Hess and flash-lag experiments [2,7,9], probably because they are initiated as soon as the visual signal drives motor activation to threshold [10]. We confirmed this with our stimuli in a further experiment in which subjects pressed a button as soon as they perceived the moving inner bar reverse direction, which occurred at an unpredictable time. The mean reaction time slope in the photopic range was 7.8 msec per log luminance, similar to the effect of luminance on perceived position. This contrasts with the synchronization task, in which the moment of response can be anticipated and the variation in visual latency can be taken into account.

One explanation for how this compensation might arise is that the visuomotor systems of our subjects had already, through life experience, been calibrated to trigger anticipated actions slightly earlier when light-levels are lower. The timing of responses intended to be synchronized with visual events can be recalibrated by artificially delayed visual feedback, and this recalibration generalizes across stimulus configurations [6]. So the finding that responses in our task were delayed only at a low luminance common in moonlight may reflect the fact that we mostly interact with moving objects during the day, and possibly that the internal dynamics of the system change when the rod photoreceptors begin to dominate [5].

The dissociation documented here may also reflect separate cortical pathways for conscious perception and the visual guidance of action [11]. If so, a hypothesis worthy of further investigation is that the visuomotor system has access to spatial representations that are corrected for varying neural delays, but which we cannot access consciously.

Supplemental Data

Supplemental data are available at http://www.current-biology.com/cgi/content/full/18/20/Rxxx/DC1

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