In the control subjects, when adaptation was restricted to one hemifield (Figure 1B), the component of the phosphene overlapping the adapted hemifield appeared coloured, and the component overlapping the unadapted hemifield was colourless. In contrast, in GY the bilateral phosphene appeared uniformly coloured after adaptation restricted to the intact field. When adaptation was restricted to GY's blind field, the phosphene always appeared colourless.

When different adapting colours were presented to the two hemifields, the bilateral phosphenes induced in the control subjects comprised both adapting colours. For instance, if the left and right hemifields were adapted to red and green, respectively, the component of the bilateral phosphene appearing in the left hemifield was red and the component appearing in the right hemifield was green. This occurred with both SOAs. The component of the phosphene overlapping with the region of the visual field where there had been a chromatic border during adaptation contained patches of both colours or appeared colourless. The former percept is similar to those reported by subjects in a study in which the retinal image was stabilized at the boundary between a pair of red and green stripes [6]. In contrast, phosphene colour in GY depended on the colour to which his intact field had been adapted. For instance, if the intact field had been adapted to red and the blind field to green, the bilateral phosphenes appeared uniformly red.

As adaptation of the blind field had no influence on phosphene colour, it must have been adaptation of the wavelength/colour-selective regions (such as V1 and V4) in the normal hemisphere that influenced phosphene colour, with interactions between the intact and damaged hemisphere providing colour perception in the blind field. Recent diffusion tensor imaging (DTI) evidence showing strong callosal connections between V5/MT regions in GY's damaged and intact hemispheres [7] support this view. The intact V1 may have played a role in determining phosphene color, as V1–V5/MT interactions within the intact hemisphere can modulate the interactions between V5/MT regions in the intact and damaged hemisphere. It is also possible that the locus of color adaptation is the LGN, as adaptation effects have been observed in this region [8,9]. V4 in the normal hemisphere could have also been involved, but the possible contribution of V4 in the damaged hemisphere is unclear, as there is no evidence on either the retinotopy of this region in GY or on its connectivity with V5/MT.

In summary, our results show that in the absence of V1, colour perception may be possible via the intact hemisphere. It has been shown previously that unconscious colour detection is possible when V1 is disrupted with TMS [10] and our results show that conscious perception of colour is also possible.

Supplemental Data

Supplemental data are available at http://www.current-biology.com/supplemental/S0960-9822(08)01056-7.

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Visuomotor timing compensates for changes in perceptual latency

Alex L. White, Daniel Linares and Alex O. Holcombe

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

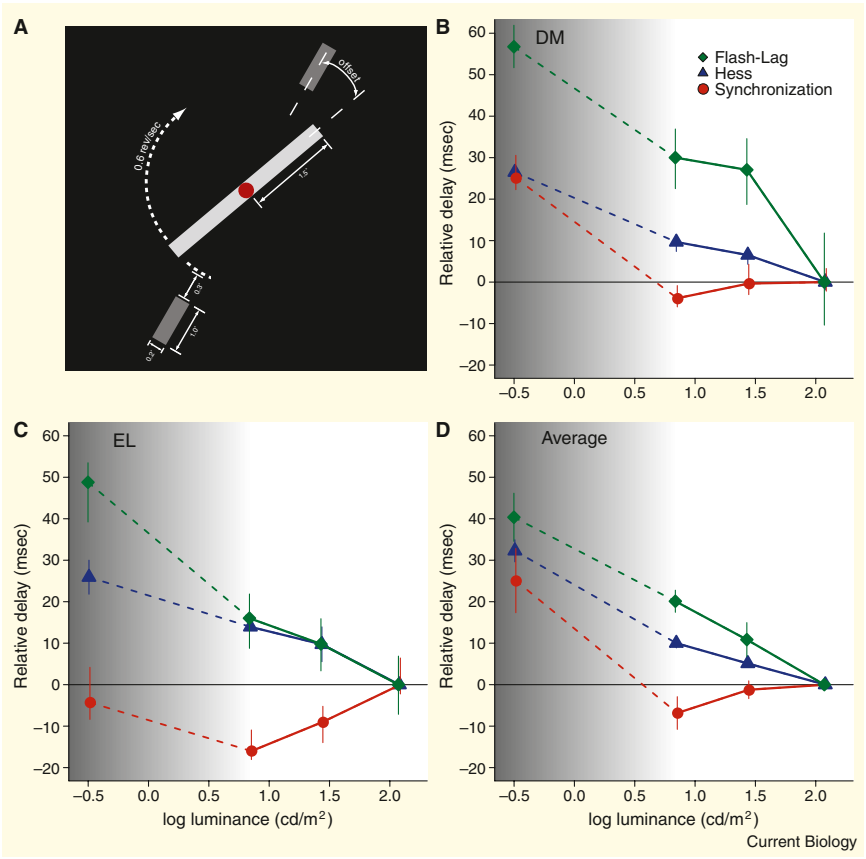

Figure 1. The stimulus display and results.

(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.

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 (red 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 of offset between the inner bar and the references varied across trials and subjects reported whether the inner bar appeared to be ahead of or behind 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 were 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/supplemental/S0960-9822(08)01099-3.

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Diversity of speed-accuracy strategies benefits social insects

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Bees face a difficult visual discrimination task when they must choose amongst dozens of species of flowers that differ in reward but look very similar. A speed-accuracy trade-off is often observed in humans and animals tested in analogous visual discrimination tasks [1,2]. Chittka *et al.* [3] showed that individual bumblebee foragers from the same colony vary in the propensity to make fast, sometimes inaccurate choices and are consistent in that propensity across situations. Unexpectedly, fast-inaccurate bees collected nectar more efficiently than slow-accurate bees [4]. Why would such behavioural variability be maintained within a colony? We suggest that behavioural variability acts to decrease variation in resource acquisition in the wild. A bet-hedging approach using a mixed group of foragers with different foraging approaches will reduce variability in nectar collection rate (NCR) because stochastic variation in forage availability is more likely to detrimentally affect a single foraging approach than multiple approaches. In turn, lower variability in NCR may help reduce the probability of extinction/colony death while overwintering [5]. Three conditions are necessary for colonies with mixed foraging strategies to outperform a colony with a single foraging strategy: first, there must be spatial or temporal heterogeneity in the distribution of rewards (we assume this to be true); second, the above heterogeneity must affect when and whether slow-accurate or fast-inaccurate strategies result in higher NCR; and third, bees must remain faithful to a particular speed-accuracy approach. Here we show that there is consistent within-colony variance between honeybee workers in their speed-accuracy approach in a flower discrimination task and that varying the proportion of rewarding flowers changes the relationship between foraging strategy and rate of nectar collection.

To test the conditions above, twelve honeybee foragers from the same colony were trained to forage at a large green table and differentiate between two types of similarly coloured (to a honeybee's visual system) artificial, round, yellow flowers that contained either 10 μL of sucrose solution (targets) or only water (distractors). After training, bees were subjected to two non-rewarding tests. The absence of reward during tests ensured the bees were not using cues from the sucrose solution to identify rewarding flowers. The order of the two tests was balanced across bees and the tests were separated by ten training landings to ensure motivation. In the High Target Frequency condition (HTF) there were three targets and three distractors (1:1 ratio rewarding to non-rewarding). In the Low Target Frequency condition (LTF) there were two targets and four distractors (1:2 ratio) and thus a relatively higher chance of encountering a non-rewarding flower.

A speed-accuracy trade-off was apparent in which foragers that spent longer times between flower visits made more accurate choices in both HTF and LTF, and bees were also consistent in their speed and accuracy of choices across tests (Figure 1A).

We estimated each bee's foraging efficiency, as if they had been foraging on rewarding flowers in the test, as: NCR = $(c \times v)/(c\,(r + i + a) + (1 - c)\,(r + a))$ where c = percent correct choices, v = nectar volume per flower (10 μL), r = inter-flower interval, i = ingestion time (estimated as 5.9 seconds [6]) and a = access time (estimated as 1 second). In the HTF condition, neither accuracy nor inter-flower intervals were correlated with NCR (Figure 1B,C). Varying access time between 1 and 10 seconds did not significantly affect the relationship between inter-flower interval and NCR, but there was a significant positive relationship between accuracy and NCR when access times were greater than 3.2 seconds (see the Supplemental data available on-line with this issue).