Cross-modal prediction changes the timing of conscious access during the motion-induced blindness

Acer Y.-C. Chang ^{a,b}, Ryota Kanai ^{b,c} & Anil K. Seth ^{a,b}

^a Department of Informatics, University of Sussex, Brighton BN1 9QJ, United Kingdom

^b Sackler Centre for Consciousness Science, University of Sussex, Brighton BN1 9QJ, United Kingdom

^c School of Psychology, University of Sussex, Brighton BN1 9QH, United Kingdom

Corresponding Author:

Acer Y.-C. Chang

Department of Informatics

University of Sussex

Brighton BN1 9QJ

United Kingdom

Phone: +44 (0)1273 606755

E-mail: ac524@sussex.ac.uk

Abstract

Despite accumulating evidence that perceptual predictions influence perceptual content, the relations between these predictions and conscious contents remain unclear, especially for cross-modal predictions. We examined whether predictions of visual events by auditory cues can facilitate conscious access to the visual stimuli. We trained participants to learn associations between auditory cues and colour changes. We then asked whether congruency between auditory cues and target colours would speed access to consciousness. We did this by rendering a visual target subjectively invisible using motion-induced blindness and then gradually changing its colour while presenting congruent or incongruent auditory cues. Results showed that the visual target gained access to consciousness faster in congruent than in incongruent trials; control experiments excluded potentially confounding effects of attention and motor response. The expectation effect was gradually established over blocks suggesting a role for extensive training. Overall, our findings show that predictions learned through cross-modal training can facilitate conscious access to visual stimuli.

Keywords:

Motion induced blindness

Predictive coding

Audiovisual association

1. Introduction

The increasingly influential framework of ‘predictive processing’ (PP) posits that the brain continuously generates and updates predictions about incoming sensory signals (Clark, 2012; Friston, 2005; Hohwy, 2013; Seth, 2014) according to principles of Bayesian inference. Accumulating empirical evidence suggests that perceptual predictions or expectations strongly influence conscious perception. For example the perceptual hysteresis effect shows that prior knowledge can enhance and stabilise conscious perception: previously perceived stimuli can bias conscious perception to represent subsequent stimuli in the same form (Hock, Scott, & Schöner, 1993; Kanai & Verstraten, 2005; Kleinschmidt, Büchel, Hutton, Friston, & Frackowiak, 2002; Williams, Phillips, & Sekuler, 1986). Recent evidence also suggests that prediction facilitates conscious access. Melloni and colleagues showed that thresholds of subjective visibility for previously seen degraded targets were lower than for novel degraded targets, with changes in threshold accompanied by a shift in a neurophysiological signature of conscious awareness to an earlier time point (Melloni, Schwiedrzik, Müller, Rodriguez, & Singer, 2011). Similarly, Lupyan and Ward (2013) found that visually presented objects preceded by congruent auditory cues (spoken words) were faster to break through continuous flash suppression than those preceded by incongruent cues. These results, and others, collectively suggest that prior knowledge can enhance and accelerate conscious access.

In the current study, we were interested in how the learning of prior expectations changes the timing of conscious access. Specifically, we asked how training of cross-modal perceptual associations influences the speed of conscious access for predicted and unpredicted events. We intensively trained participants to learn a cross-modal predictive relationship between an auditory tone and a colour change of a visual target, and we tested in separate experimental sessions how the learned predictive association affected the timing of conscious access of the visual target. Training phases and test phases were interleaved in order to explore the temporal nature of the influence of cross-modal perceptual predictions on conscious access

To precisely measure the timing of conscious access in the test phases, we employed the well-known motion-induced blindness (MIB) paradigm (Bonneh, Cooperman, & Sagi, 2001). In MIB, a peripheral visual target disappears and reappears from awareness periodically when it is presented superimposed on a rotating background pattern. Because disappearances and reappearances are clear-cut in MIB (as compared to, for instance, binocular rivalry), participants can reliably report the timing of conscious access to the target. Previous research using MIB has shown that subjectively unseen visual information can still be integrated and updated to form new

object representations unconsciously (Mitroff & Scholl, 2005). More recently, Wu and colleagues demonstrated that a transient visual change (a flashed ring) can influence the timing of conscious access of an unseen target (Wu, Busch, Fabre-Thorpe, & VanRullen, 2009). These findings speak to the persistence of representations of target stimuli during periods of subjective invisibility during MIB. We hypothesised that conscious access to such representations could be influenced by cross-modal cues if strong associations were formed via extensive training. To test this, we delivered an auditory cue while visual target was rendered subjectively invisible via MIB, and we then gradually changed the colour of the target to assess how the congruency between the cue and the visual sensory event influenced the timing of subjective target reappearance. Timing was compared with that from control trials in which the target was physically removed. In this way, we were able to quantify the effects of prediction on awareness and while minimizing the impact of other cognitive process such as attention and response bias.

2. Methods

2.1. *Participants*

Participants were 26 healthy students from the University of Sussex (7 male, 18–31 years; mean age 23.15 years, normal or corrected-to-normal vision). All of them provided informed consent before the experiment and received £15 or course credits as compensation. Two participants were excluded from data analysis because they misunderstood the instructions as to key responses. The experiment was approved by the University of Sussex ethics committee.

2.2. *Stimuli and Procedure*

Stimuli were generated using the Psychophysics toolbox (Brainard, 1997) and all visual stimuli were presented on a Dell Trinitron CRT calibrated display (resolution 1048x768; refresh rate 100 Hz) with a black background. Participants sat 50 cm away from the monitor. A linearized colour lookup table was used for gamma correction ($\gamma = 2.2$).

Participants took part in a total of 4 training blocks and 4 MIB (testing) blocks across two consecutive days. As shown in Figure 1, each participant completed four interleaved training and MIB block on each day as follows: (i) Training (200 trials); (ii) MIB (90 trials); (iii) Training (100 trials); (iv) MIB (90 trials).

The training procedure. At the beginning of a training trial, participants were presented with a white fixation point and a blue target stimulus (Figure 2). The fixation point and the target were both circular dots subtending 0.2 degrees of visual angle. The fixation was presented at the centre

of the screen and the target was to the upper-left of the fixation at 5.4 degrees of visual angle. Participants were instructed to maintain their gaze at the central fixation point and to pay attention to the peripheral target during the entire trial. Following a delay (drawn from a random uniform distribution of 1-2 sec) an auditory cue (500 Hz or 1000 Hz pure tone) was presented for 300 ms. One second following the auditory cue onset, the target changed its colour (instantaneously) from its initial blue to either red or green. Crucially, the pitch of the auditory cue predicted the colour change with 80% validity. For example, after the 500Hz tone there was an 80% chance of a blue-to-red colour change and a 20% chance of a blue-to-green change. In this *training* task, participants were required to indicate the new colour of the target by pressing key ‘.>’ (with the right index finger) or ‘/?’ (with the right middle finger) as accurately and fast as possible. Feedback was presented on the screen after each correct and incorrect trial. The probability mapping between the cue and the colour change of the target, and the mapping between the colour changes and the response keys, were counterbalanced between participants.

The MIB procedure. In the MIB blocks (Figure 3a and 3b), each trial also started with a central fixation point and a peripheral target. To induce MIB of the peripheral target, we presented a rotating pattern consisting of an array of 64 (8 x 8) grey crosses occupying 15.6°x15.6° in the background. The speed of rotation was 0.5 cycle/s. The rotating background temporarily induced the subjective disappearance of the target, this being MIB. Participants were instructed to indicate the target disappearance and reappearance by pressing and releasing the ‘z’ key respectively (with the left index finger). Immediately after the report of disappearance, the colour of the target started changing gradually and linearly in RGB space from blue to green or red. The complete colour change took 3 seconds. While this colour change was occurring, 1 second after target disappearance, a 500 Hz or 1000 Hz tone was delivered to the participants. The participants were instructed to ignore the tone and to release the key as quickly as possible following subjective reappearance of the target. The target remained on the screen for 300 ms after the key was released. This was followed by a colour judgement task in which participants had to report the new colour of the target with the same response keys as in the training block. In cases where participants released the key before the colour change had completed, they were instructed to indicate whether the colour was closer to red or green. This response ended the trial. If participants released the key (signifying subjective target reappearance) before auditory cue presentation, the trial was discarded. The probabilistic relationship between the pitch of the tone and the change of the colour remained the same as the training procedure (80%). The time to reappearance, defined as the duration between the onset of the cue and reappearance of the target reported by key release, was used to measure the influence of prediction on the timing of conscious awareness of the target. Before the first MIB block started, participants performed

several practice trials (> 20) to learn how to acclimatise to the MIB procedure in order to ensure they reliably experienced long periods of target invisibility.

To exclude the effects of attentional bias and congruency effects at a response stage, participants undertook control trials in which the target was physically removed from the stimulus display (Figure 3c). Participants followed the same instruction in the control trials as in experimental trials: They needed to indicate the disappearance and reappearance of the target and make a subsequent target colour judgement. To match the individual MIB behavioural profiles, control trials were designed as ‘replays’ of experimental trials within the same block: Durations of subjective invisibility and reappearance colours were sampled from the within-block experimental trials. Each sampled experimental trial was used to construct four congruent control trials and one incongruent control trial. These control trials were randomly inserted into the remaining period of the same block. The duration between the onset of a trial and the onset of the physical disappearance was randomly selected between 2 to 4 seconds for each control trial. Each MIB block consisted of 60 randomly interleaved experimental trials and 30 control trials.

After completing the fourth MIB block, participants completed a brief questionnaire concerning the subjective evaluation of the influence of the auditory cue on the disappearance duration of the visual target (a 5-point-scale question “Do you feel that the pitch of the sound influenced your perception of the target during the MIB state? From “1-not at all” to “5-I strongly felt the influence”).

3. Results

In the training blocks, analysis of response times (RTs) indicated that participants successfully learned the tone-colour probabilistic association. We defined the blockwise *congruency effect* (dependent variable) as the mean RTs of incongruent trials minus the mean of congruent trials, for a given block. The congruency effects of each block were submitted to Bonferroni-corrected one-tailed one-sample t-tests. We found that all congruency effects were significantly higher than 0 (all corrected $ps < 0.05$, see Figure 4). This indicates that participants learned the statistical relationship between the cue and the target in all training blocks. The mean accuracy in the training block was 97.65% (SD = 2.03%) and all participants showed above 90% mean accuracy. The high accuracy indicates participants correctly performed the task.

We next analysed the MIB blocks. The top panel of Figure 5 shows the mean time-to-reappearance in each condition. The overall time-to-reappearance in control trials was longer than in experimental trials (1780 and 1114 ms respectively, $t(23) = -14.78$, $p < .001$). This

was expected due to the ‘replay’ nature of the control trials, which ensures that the response time for the experimental trials provides a lower bound on the response times possible in the control trials (excluding errors).

To test if the learned associations modulated timing of conscious access in the MIB blocks, we similarly defined the blockwise congruency effect as the mean time-to-reappearance of incongruent trials minus the mean time-to-reappearance of congruent trials. First, we found significant differences across block (one-way repeated-measure ANOVA with the four-level factor Block, $F(3, 69) = 3.20, p = .03, \eta^2 = .12$). Next, polynomial contrasts revealed a strong linear trend in congruency effect from block 1 to block 4, $F(1, 23) = 6.91, p = .015, \eta^2 = .23$ (

Figure 5, lower panel). Post hoc analyses revealed a significant difference between block 1 and 3, $t(23) = 2.90, p < .01$, and block 1 and 4, $t(23) = 2.34, p = .028$. These results indicate that the congruency effect in the MIB condition increased with successive blocks of training. No significant congruency effect was found by ANOVA and polynomial contrast analysis in any control blocks (all $ps > 0.5$). The same results were replicated by the median time-to-reappearance, indicating that the congruency effect change was not dominated by outliers (see Supplementary Material). Thus, the learned cross-modal associations significantly accelerated conscious access, with this influence reliably increasing over time.

To ensure the results were not driven by outlying participants, we tested whether the congruency effect change was consistent across participants by adopting a general linear model (GLM) approach to estimate congruency effect at the individual level. For each participant, a GLM with one regressor (congruent versus incongruent) was applied to each block to estimate the congruency effect. The standardised regression coefficient of each block and each participant (i.e., beta) was computed and entered into the group level analysis as a dependent variable. The results of this analysis are highly comparable to the results computed by the mean time-to-reappearance difference as mentioned above. First, we found significant differences across block (one-way repeated-measure ANOVA with the four-level factor Block, $F(3, 69) = 4.4, p < .01, \eta^2 = .161$). Next, a polynomial contrast performed on betas revealed a strong linear trend in congruency effect from block 1 to block 4, $F(1, 23) = 11.26, p < .01, \eta^2 = .329$. Post hoc analyses revealed significant differences between block 1 and 2, $t(23) = 2.07, p = .05$, 1 and 3, $t(23) = 3.02, p < .01$, and block 1 and 4, $t(23) = 3.2, p < .01$. No significant congruency effect was found by ANOVA and polynomial contrast analysis in any control blocks (all $ps > 0.3$). The results indicate that the congruency effect change across blocks was reproducible at an individual-participant level.

To further establish that these congruency effects in the MIB blocks were associated

specifically with the tone-colour training, we performed an additional analysis. We reasoned that if the changes of the congruency effects from the first MIB block to the fourth block were influenced by the training, then the magnitude of changes in congruency effect over the training blocks should predict the magnitude of changes of congruency effect during the experimental sessions. To balance training trial numbers in this analysis, we calculated the magnitude of mean congruency effect in the first two blocks and last two blocks and the difference between the two means for both training and MIB trials, and then examined the correlation in the differences across participants. Results confirmed our prediction. Applying a Spearman's rank correlation test, we found a significant correlation ($\rho = .45$, $p = .026$, see Figure 6) indicating a linear relationship between the change of association strength and the change of influence of prediction on conscious awareness as indexed by congruency effect. There was no significant correlation when the same analysis was applied to control trials ($\rho = -0.16$, $p = .43$).

To exclude any possible confound due to problems in discriminating target colour on reappearance, we computed the mean accuracy of the colour judgement in the MIB. The accuracy was nearly perfect (99.23%, $SD = .7\%$) indicating that participants did not have difficulty in discriminating the colour upon reappearance. Due to the ceiling effect, we did not observe any significant differences in accuracy between the congruent and incongruent conditions in both experimental and control trials (all p -values $> .38$).

Finally, to test whether participants were aware of the influence of prediction on the time-to-reappearance, we computed the correlation between the self-evaluation scores from the post-experiment questionnaire and the congruency effects. We did not find a significant relationship between them ($r = -.253$, $p = .233$), suggesting that participants' self-evaluation of the influence of the pitch was independent from the actual strength of influence from the predictive cues.

4. Discussion

We have described psychophysical data showing that learned cross-modal associations influence the timing of conscious access during motion-induced blindness. In an interleaved training-testing design we trained participants to learn associations between tones and colours, and then – using tones as predictive cues – explored whether congruent tone cues modulated the subjective timing of reappearance of coloured target stimuli. The results showed that cross-modal predictive cueing accelerated time to conscious access, but only after extensive training. We found

a linear relationship between the amount of training and the degree of facilitation, further underlining that learning of predictive associations can regulate their influence on the timing of conscious access. This finding was further supported by a correlation between the individual improvements in prediction learning from day one to day two, with the magnitude of the prediction effect across the same time period.

Crucially, our design allowed us to exclude that the effects of prediction on the timing of conscious access were due to motor preparation or feature-based attention. First, the procedures and task goals were different for training and MIB blocks. In the training blocks, the task was to detect the colour change of target and to respond by pressing one of two keys to report the colour. In the MIB blocks, the task was to detect the reappearance of the target and to respond via a single key press. This difference in task makes it unlikely that participants adapted a similar motor preparation strategy acquired during the training to the MIB blocks. Second, it is well known that feature-based attention can facilitate the visual processing and detection performance of attended target features (Maunsell & Treue, 2006). One might wonder whether the prediction effect we found in the MIB blocks could be attributed to the facilitation of feature-based attention triggered by the auditory cue to a specific target colour. However, our control trials exclude this possibility, because the control trials were designed to replicate the subjective experience of the experimental trials but with physical disappearance and reappearance of the target from the stimulus array. In both experimental and control trials, participants performed the same task (detection of target reappearance). Crucially in these control trials, we found no difference in subjective time-to-reappearance between congruent and incongruent trials. Therefore, feature-based attention cannot account for the congruency effects of predictions on the timing of conscious access in our paradigm. In sum, our results taken together support that learned cross-modal predictive associations were responsible for the shift in the timing of conscious access.

One important innovation of our study is the demonstration of the flexibility that *arbitrary, cross-modal* predictions can influence the timing of access to subjectively suppressed visual information through training. Previous studies focus on the prediction between long-term bound representations, e.g. semantic-object identity (Chen, Yeh, & Spence, 2011; Lupyan & Ward, 2013) or audiovisual speech (Alsius & Munhall, 2013; Palmer & Ramsey, 2012) and motion integration (Conrad, Bartels, Kleiner, & Noppeney, 2010). For example, Conrad and colleagues (Conrad et al., 2010) show that, in binocular rivalry, motion sounds can stabilise and lengthen dominance periods for congruent visual motion. Similarly, Chen, Yeh, and Spence found that auditory cues shortened the suppression period of congruent visual objects. Taken together, these findings suggest that cross-modal predictive information exerts substantial influences on unconscious processing,

conscious perception, and their interaction.

It is known that saccadic eye movements during MIB can cause immediate target reappearance. Previous research have also shown that microsaccades can modulate target perceptual transitions (Bonneh et al., 2009; Hsieh & Tse, 2009; Martinez-Conde, Macknik, Troncoso, & Dyar, 2006). Based on these previous findings, one might wonder whether our results might be explained by eye movements occurring preferentially when colour changes were congruent with auditory cues. We first note that participants were asked to maintain fixation during each trial, so saccades could be expected to be rare. In addition, in our experiment, colour changes happen both gradually and during perceptual suppression by MIB, making it is highly unlikely such eye movements could be triggered in such specific manner. Additionally, during data analysis, we discarded those trials in which the target reappearance *preceded* the predictive sound onset, where plausibly saccadic effects could have caused target reappearance. To sum up, the current result was unlikely caused by any impact of eye-movement.

What implications do our results have for possible neural mechanisms? One possibility is that cross-modal predictions modulate the strength of low-level cortical stimulus representations. Recent findings by Kok, de Lange, and colleagues show that learned auditory to visual predictions can create a neuronal template of the expected visual stimulus in the visual cortex (Kok, Failing, & de Lange, 2014) and bias visual representations as a result of the facilitation of information processing for the expected stimulus (Kok, Brouwer, Gerven, & de Lange, 2013). This direct impact from cross-modal prediction to low-level visual representations may lead to a change in timing of conscious access, especially if these visual representations can be construed as a stimulus specific priors in a Bayesian framework. More generally our results strongly indicate the existence of neural pathways capable of conveying cross-modal predictive information. Previous studies have shown that, during associative learning, brain connectivity between cortical regions responsible for associated events increases in strength with training (Büchel, Coull, & Friston, 1999; McIntosh & Gonzalez-Lima, 1998; Ouden, Friston, Daw, McIntosh, & Stephan, 2009; von Kriegstein & Giraud, 2006). This suggests the possibility that, in the current study, the incremental change of the facilitation effect may be due to a gradual build-up of functional connectivity for conveying predictive information across the sensory modalities. Future investigations combining psychophysics with neuroimaging connectivity analyses could test this hypothesis.

In the current study, the congruency effect in the second day MIB blocks (the block 3 and 4) was much stronger than that in the first day MIB blocks (the block 1 and 2). A potential explanation for the second day ‘boost’ is that sleep between the two days facilitated and consolidated the

associative learning from the first day. It is well known that sleep plays a beneficial role in memory consolidation (Stickgold & Walker, 2007; Walker & Stickgold, 2006) as previous studies have shown sleep facilitates associative memory (Stickgold, Scott, Rittenhouse, & Hobson, 1999), statistical learning (Durrant, Taylor, Cairney, & Lewis, 2011), and perceptual learning (Fenn, Nusbaum, & Margoliash, 2003; Karni, Tanne, Rubenstein, Askenasy, & Sagi, 1994; Stickgold, James, & Hobson, 2000; Yotsumoto et al., 2009). In the current study, participants learned the statistical relationship between the auditory cue and the visual target. Given the extent literature on the role of sleep in learning, it is plausible that sleep strengthened the predictive value of the auditory cues, thereby facilitating conscious access to predicted visual events on the second day. However, in the current study was not explicitly designed to examine the effect of sleep in our experimental paradigm. Thus, we leave this possibility open for future studies.

Our results lend support to predictive coding (or predictive processing) frameworks for understanding perception (Clark, 2012; Friston, 2005; Rao & Ballard, 1999). On these views, perceptual content is determined by probabilistic inference of the most likely external causes of sensory signals. Our data support the view that conscious access occurs when predictive models are verified against sensory inputs so that prediction errors are minimized. On this view, valid predictive cues will engage predictive models that are validated against sensory signals more rapidly, leading to more rapid conscious access (Lupyan & Ward, 2013; Melloni et al., 2011). The present results extend this approach by showing how predictive influences on perception develop across time via training, and by underlining the flexibility of these influences by demonstrating their efficacy using cross-modal and arbitrary associations. These results together suggest that predictive influences may permeate and shape conscious experiences more deeply and broadly than previously thought.

Acknowledgments

Acer Y.-C. Chang is supported by a graduate teaching assistantship from the School of Engineering and Informatics at the University of Sussex, by a scholarship provided by Sackler Centre for Consciousness Science, and by the ministry of education Republic of China. Anil K. Seth is supported by the Dr. Mortimer and Dame Theresa Sackler Foundation and by ERC project CEEDS (FP7-ICT-258749). Ryota Kanai is supported by PRESTO grant from Japan Science and Technology Agency (JST).

References

- Alsius, A., & Munhall, K. G. (2013). Detection of Audiovisual Speech Correspondences Without Visual Awareness. *Psychological Science*, 24(4), 423–431. doi:10.1177/0956797612457378
- Bonneh, Y., Cooperman, A., & Sagi, D. (2001). Motion-induced blindness in normal observers. *Nature*, 411(6839), 798–801. doi:10.1038/35081073
- Bonneh, Y., Sagi, D., Cooperman, A., Tobias Donner, Heeger, D., Fried, M., & Arieli, A. (2009). Motion-induced blindness and microsaccades: Cause or effect? *Journal of Vision*, 9(8), 289–289. doi:10.1167/9.8.289
- Brainard, D. H. (1997). The Psychophysics Toolbox. *Spatial Vision*, 10(4), 433–436. doi:10.1163/156856897X00357
- Büchel, C., Coull, J. T., & Friston, K. J. (1999). The Predictive Value of Changes in Effective Connectivity for Human Learning. *Science*, 283(5407), 1538–1541. doi:10.1126/science.283.5407.1538
- Chen, Y.-C., Yeh, S.-L., & Spence, C. (2011). Crossmodal constraints on human perceptual awareness: auditory semantic modulation of binocular rivalry. *Frontiers in Psychology*, 2, 212. doi:10.3389/fpsyg.2011.00212
- Clark, A. (2012). Whatever Next? Predictive Brains , Situated Agents , and the Future of Cognitive Science . *Behavioral and Brain Sciences*, 1–86.
- Conrad, V., Bartels, A., Kleiner, M., & Noppeney, U. (2010). Audiovisual interactions in binocular rivalry. *Journal of Vision*, 10(10). doi:10.1167/10.10.27
- Fenn, K. M., Nusbaum, H. C., & Margoliash, D. (2003). Consolidation during sleep of perceptual learning of spoken language. *Nature*, 425(6958), 614–616. doi:10.1038/nature01951
- Friston, K. (2005). A theory of cortical responses. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 360(1456), 815–836. doi:10.1098/rstb.2005.1622
- Hock, H. S., Scott, J., & Schöner, G. (1993). Bistability and hysteresis in the organization of apparent motion patterns. *Journal of Experimental Psychology: Human Perception and Performance*, 19(1), 63–80. doi:10.1037/0096-1523.19.1.63
- Hohwy, J. (2013). *The Predictive Mind*. Oxford University Press.
- Hsieh, P.-J., & Tse, P. U. (2009). Microsaccade Rate Varies with Subjective Visibility during Motion-Induced Blindness. *PLoS ONE*, 4(4), e5163. doi:10.1371/journal.pone.0005163
- Kanai, R., & Verstraten, F. A. J. (2005). Perceptual manifestations of fast neural plasticity: Motion priming, rapid motion aftereffect and perceptual sensitization. *Vision Research*, 45(25–26), 3109–3116. doi:10.1016/j.visres.2005.05.014

- Karni, A., Tanne, D., Rubenstein, B. S., Askenasy, J. J., & Sagi, D. (1994). Dependence on REM sleep of overnight improvement of a perceptual skill. *Science*, 265(5172), 679–682.
doi:10.1126/science.8036518
- Kleinschmidt, A., Büchel, C., Hutton, C., Friston, K. J., & Frackowiak, R. S. . (2002). The Neural Structures Expressing Perceptual Hysteresis in Visual Letter Recognition. *Neuron*, 34(4), 659–666. doi:10.1016/S0896-6273(02)00694-3
- Kok, P., Brouwer, G. J., Gerven, M. A. J. van, & de Lange, F. P. (2013). Prior Expectations Bias Sensory Representations in Visual Cortex. *The Journal of Neuroscience*, 33(41), 16275–16284. doi:10.1523/JNEUROSCI.0742-13.2013
- Kok, P., Failing, M. F., & de Lange, F. P. (2014). Prior Expectations Evoke Stimulus Templates in the Primary Visual Cortex. *Journal of Cognitive Neuroscience*, 1–9.
doi:10.1162/jocn_a_00562
- Lupyan, G., & Ward, E. J. (2013). Language can boost otherwise unseen objects into visual awareness. *Proceedings of the National Academy of Sciences*. doi:10.1073/pnas.1303312110
- Martinez-Conde, S., Macknik, S. L., Troncoso, X. G., & Dyar, T. A. (2006). Microsaccades Counteract Visual Fading during Fixation. *Neuron*, 49(2), 297–305.
doi:10.1016/j.neuron.2005.11.033
- Maunsell, J. H. R., & Treue, S. (2006). Feature-based attention in visual cortex. *Trends in Neurosciences*, 29(6), 317–322. doi:10.1016/j.tins.2006.04.001
- Mcintosh, A. R., & Gonzalez-Lima, F. (1998). Large-Scale Functional Connectivity in Associative Learning: Interrelations of the Rat Auditory, Visual, and Limbic Systems. *Journal of Neurophysiology*, 80(6), 3148–3162.
- Melloni, L., Schwiedrzik, C. M., Müller, N., Rodriguez, E., & Singer, W. (2011). Expectations Change the Signatures and Timing of Electrophysiological Correlates of Perceptual Awareness. *The Journal of Neuroscience*, 31(4), 1386–1396.
doi:10.1523/JNEUROSCI.4570-10.2011
- Mitroff, S. R., & Scholl, B. J. (2005). Forming and updating object representations without awareness: evidence from motion-induced blindness. *Vision Research*, 45(8), 961–967.
doi:10.1016/j.visres.2004.09.044
- Ouden, H. E. M. den, Friston, K. J., Daw, N. D., McIntosh, A. R., & Stephan, K. E. (2009). A Dual Role for Prediction Error in Associative Learning. *Cerebral Cortex*, 19(5), 1175–1185.
doi:10.1093/cercor/bhn161
- Palmer, T. D., & Ramsey, A. K. (2012). The function of consciousness in multisensory integration. *Cognition*, 125(3), 353–364. doi:10.1016/j.cognition.2012.08.003

- Rao, R. P., & Ballard, D. H. (1999). Predictive coding in the visual cortex: a functional interpretation of some extra-classical receptive-field effects. *Nature Neuroscience*, 2(1), 79–87. doi:10.1038/4580
- Seth, A. K. (2014). A predictive processing theory of sensorimotor contingencies: Explaining the puzzle of perceptual presence and its absence in synesthesia. *Cognitive Neuroscience*, 1–22. doi:10.1080/17588928.2013.877880
- Stickgold, R., James, L., & Hobson, J. A. (2000). Visual discrimination learning requires sleep after training. *Nature Neuroscience*, 3(12), 1237–1238. doi:10.1038/81756
- Stickgold, R., Scott, L., Rittenhouse, C., & Hobson, J. A. (1999). Sleep-Induced Changes in Associative Memory. *Journal of Cognitive Neuroscience*, 11(2), 182–193. doi:10.1162/089892999563319
- Stickgold, R., & Walker, M. P. (2007). Sleep-dependent memory consolidation and reconsolidation. *Sleep Medicine*, 8(4), 331–343. doi:10.1016/j.sleep.2007.03.011
- Von Kriegstein, K., & Giraud, A.-L. (2006). Implicit Multisensory Associations Influence Voice Recognition. *PLoS Biol*, 4(10), e326. doi:10.1371/journal.pbio.0040326
- Walker, M. P., & Stickgold, R. (2006). Sleep, Memory, and Plasticity. *Annual Review of Psychology*, 57(1), 139–166. doi:10.1146/annurev.psych.56.091103.070307
- Williams, D., Phillips, G., & Sekuler, R. (1986). Hysteresis in the perception of motion direction as evidence for neural cooperativity. *Nature*, 324(6094), 253–255. doi:10.1038/324253a0
- Wu, C.-T., Busch, N. a, Fabre-Thorpe, M., & VanRullen, R. (2009). The temporal interplay between conscious and unconscious perceptual streams. *Current Biology*: CB, 19(23), 2003–7. doi:10.1016/j.cub.2009.10.017
- Yotsumoto, Y., Sasaki, Y., Chan, P., Vasios, C. E., Bonmassar, G., Ito, N., ... Watanabe, T. (2009). Location-Specific Cortical Activation Changes during Sleep after Training for Perceptual Learning. *Current Biology*, 19(15), 1278–1282. doi:10.1016/j.cub.2009.06.011

Figure Captions

Figure 1

Organization of the experiment. Participants took part in two sessions on two consecutive days. Each session consisted of two 'training' and two 'MIB' blocks. Each MIB block consisted of 60 experimental trials interleaved with a block of 30 control trials.

Figure 2

The trial sequence during training blocks. A fixation and a target (the blue dot) display were presented for 1,000 to 2,000 ms and followed by a 300 ms auditory cue (500Hz or 1000Hz). 1000 ms following the auditory cue, a colour change of the target occurred. Participants were instructed to respond to this colour change by pressing a key. The right panel illustrates the probabilistic relationships between the frequencies of the tone and the change of colours of the target.

Figure 3

The trial sequence during motion-induced blindness (MIB) blocks: (a) the subjective perceived sequence (b) the experimental sequence. (c) the control sequence. Each MIB experimental trial (a, b) started with a central fixation point, a peripheral target, and a constantly rotating background. The rotating background temporarily induced the subjective disappearance of the target and participants were instructed to indicate subjective disappearance and reappearance times by pressing and releasing a key. After the key was pressed (i.e., the onset of subjective invisibility), the colour of the target started changing gradually from blue to green (or red); the complete change lasted 3 seconds. 1 second after the start of this colour change, a 500

Hz or 1000 Hz tone (the cue) was delivered. The reappearance duration, defined as the duration between the onset of the cue and the key release was used to estimate the influence of the prediction on the conscious awareness of the target. At the end of a trial, participants were instructed to indicate whether the colour was more similar to pure red or pure green. In a control trial (c), participants followed the same instruction in as in experimental trials. However, the target was physically removed from the stimulus display. (d) The time course of colour change in the experimental sequence. Note that the colours are highly distinguishable at the (average) reappearance time.

Figure 4

Response times (RTs) in the training blocks. The congruency effect was defined as the mean RTs of incongruent trials minus the mean RTs of congruent trials. Bonferroni corrected one-sample t-tests indicate that the congruency effect was significantly greater than zero in all the four training blocks. This indicates that participants learned the statistical relationship between the cue and the target at the very beginning of the experiment and maintained the learned association across the four training blocks. Error bars represent one standard error of the mean across participants. (* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$)

Figure 5

The upper panel show mean time-to-reappearance in each condition, and by block. The lower panel shows the corresponding congruency effects. The congruency effect showed a linear trend increment from Block 1 to Block 4 for experimental trials (left) but not for control trials (right). Post-hoc t-tests revealed that congruency effects in Block 3 and 4 were significantly larger than in Block 1. Error bars represent standard errors. (* $P < 0.05$, ** $P < 0.01$)

Figure 6

A Spearman's rank correlation test on MIB congruency change and the training congruency effect change between the first (the block 1 and 2) and the second half (the block 3 and 4) of the experiment. Data from the experimental trials showed a significant correlation. No effect was found in the control trials.