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SHORT REPORT

Dissociation of prediction from conscious perception

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Abstract. The framework of predictive coding offers a parsimonious explanation for many perceptual phenomena. According to this framework, perception of the outer world is created by the comparison of incoming sensory information with an internal predictive model based on previous experience and context. However, it is unclear whether the predicted percept needs to enter conscious awareness for the internal predictive model to be effective. Here we used an apparent motion paradigm to show that while prediction and conscious awareness of a predicted percept may coincide, a dissociation can be observed. When sensory information provides reliable input for the internal predictive model, the predicted percept does not have to be consciously perceived for successful prediction. However, when sensory input is ambiguous, conscious awareness helps the prediction to take effect.

Keywords: visual predictions, conscious perception, predictive coding, apparent motion, vision, awareness

1 Introduction

The theoretical framework of predictive coding provides a parsimonious explanation for many perceptual phenomena and their emergence into conscious awareness (Clark, 2013; Friston, 2010; Hohwy, Roepstorff, & Friston, 2008; Melloni, Schwiedrzik, Müller, Rodriguez, & Singer, 2011). In this framework the brain predicts the characteristics of the outer world by comparing incoming sensory information with an internal model of the world constrained by previous experience and context. However, it is unclear so far to what extent the predicted percept has to enter conscious awareness for the predictive model to work successfully—in other words, does conscious perception influence predictions? To study this experimentally, we exploited the well-known illusion of long-range apparent motion. Here, two visual stimuli presented in rapid succession create the illusion, or prediction, of a single moving token (Alink, Schwiedrzik, Kohler, Singer, & Muckli, 2010; Muckli, Kohler, Kriegeskorte, & Singer, 2005). Depending on individual differences and the distance and frequency at which the stimuli are flashed, the stimuli can be perceived as smooth illusory motion or as two simultaneously flickering dots. To measure the spatiotemporal prediction of the illusory motion token, we flashed targets on the apparent motion path, either in time or out of time with the illusory token. In-time targets fit the spatiotemporal prediction and are usually detected more frequently than out-of-time targets not fitting the prediction, as we demonstrated previously (Schwiedrzik, Alink, Kohler, Singer, & Muckli, 2007; Vetter, Edwards, & Muckli, 2012; Vetter, Grosbras, & Muckli, in press). Our paradigm is useful to study predictive coding in the visual system as it taps directly into a circumscribed spatiotemporal prediction—predictable (in-time) targets are more readily perceived than unpredictable (out-of-time) targets. Here we investigated whether this predictability effect depends on the conscious perception of the apparent motion illusion, or whether prediction (of in-time targets) is also successful when apparent motion is not perceived—that is, when only flicker is perceived. To this aim, we exploited the fact that conscious perception of apparent motion varies depending on apparent motion frequencies and individual differences (ie for each individual there is an optimal frequency range for apparent motion perception). Thus, we measured the detection of predictable and unpredictable targets depending on subjects' report of conscious apparent motion perception at different apparent motion frequencies. We hypothesised that if predictable (in-time) targets have a detection advantage regardless of subjects' apparent motion perception and regardless of apparent motion frequency, then prediction can act independently from conscious awareness. Alternatively, if the detection advantage of predictable targets varies across apparent motion frequencies and as a function of conscious perception of apparent motion, then prediction can be enhanced or impaired by conscious awareness.

Note that we did not compare predictable versus unpredictable target detection in the presence and absence of consciousness per se. Instead, we investigated whether the spatiotemporal prediction on the apparent motion path depends on the conscious awareness of the percept that accompanies the motion prediction (smooth apparent motion).

2 Results

Apparent motion was induced by flashing two white squares alternatively at four different frequencies (F1: 1.88 Hz, F2: 2.68 Hz, F3: 3.75 Hz, F4: 4.69 Hz), and targets were flashed on the apparent motion trace either in time or out of time with the illusory motion token (see section 4 and figure 1; Schwiedrzik et al., 2007; Vetter et al., 2012; Vetter et al., in press). After each trial, subjects reported on whether they detected the target and whether they perceived apparent motion. Subjects reported smooth apparent motion perception on average in 53.9% (SEM = 4.13) of all trials, with a slight modulation across frequencies [F1: 50.6% (7.8); F2: 64.5% (7.1); F3: 55.4% (8.5); F4: 45.0% (9.8); repeated-measures ANOVA: $F_{3,42} = 3.19$, $p = 0.033$].

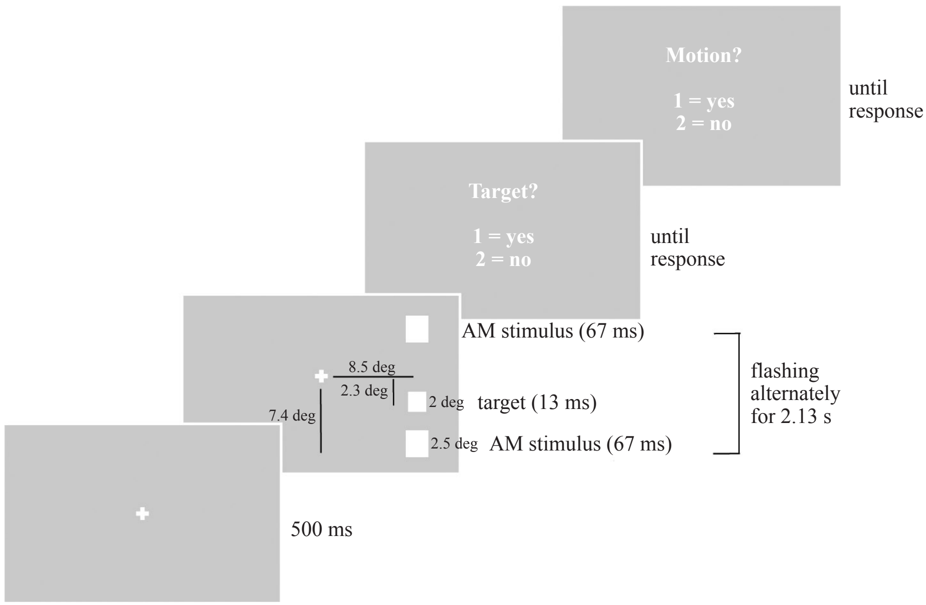

Figure 1. Stimuli and experimental design. Apparent motion (AM) was induced by flashing two white squares (AM stimuli) in rapid succession at four different frequencies (1.88 Hz, 2.68 Hz, 3.75 Hz, 4.69 Hz, pseudorandomised). A target was flashed on the apparent motion trace either in time or out of time with the illusory motion token—that is, either fitting the spatiotemporal prediction or not. Subjects' task was to detect the target and to report on their conscious perception of smooth apparent motion.

Trials were divided into those with motion and no motion perception. As previously observed (Schwiedrzik et al., 2007; Vetter et al., 2012; Vetter et al., in press), predictable in-time targets were detected better than unpredictable out-of-time targets (see figure 2a for absolute detection rates of both target types and across frequencies). There was a main effect of predictability both when motion was perceived ($F_{1,14} = 26.6$, $p < 0.001$) and when motion was not perceived ($F_{1,14} = 10.6$, $p = 0.006$). No main effect of perceived motion ($p > 0.1$) was observed when analysing all data together. Figure 2b depicts our crucial measure of the predictability effect, expressed as the mean relative difference between in-time and out-of-time detection rate: hit rate (in time) − hit rate (out of time)/[hit rate (in time) + hit rate (out of time)]—it is positive when in-time targets are detected better than out-of-time targets. When motion was perceived, mean relative accuracy differences did not vary across apparent motion frequencies ($F_{3,42} = 0.12$, $p > 0.1$). However, when motion was not perceived, the effect of better in-time target detection was modulated by frequency ($F_{3,42} = 6.6$, $p = 0.001$).

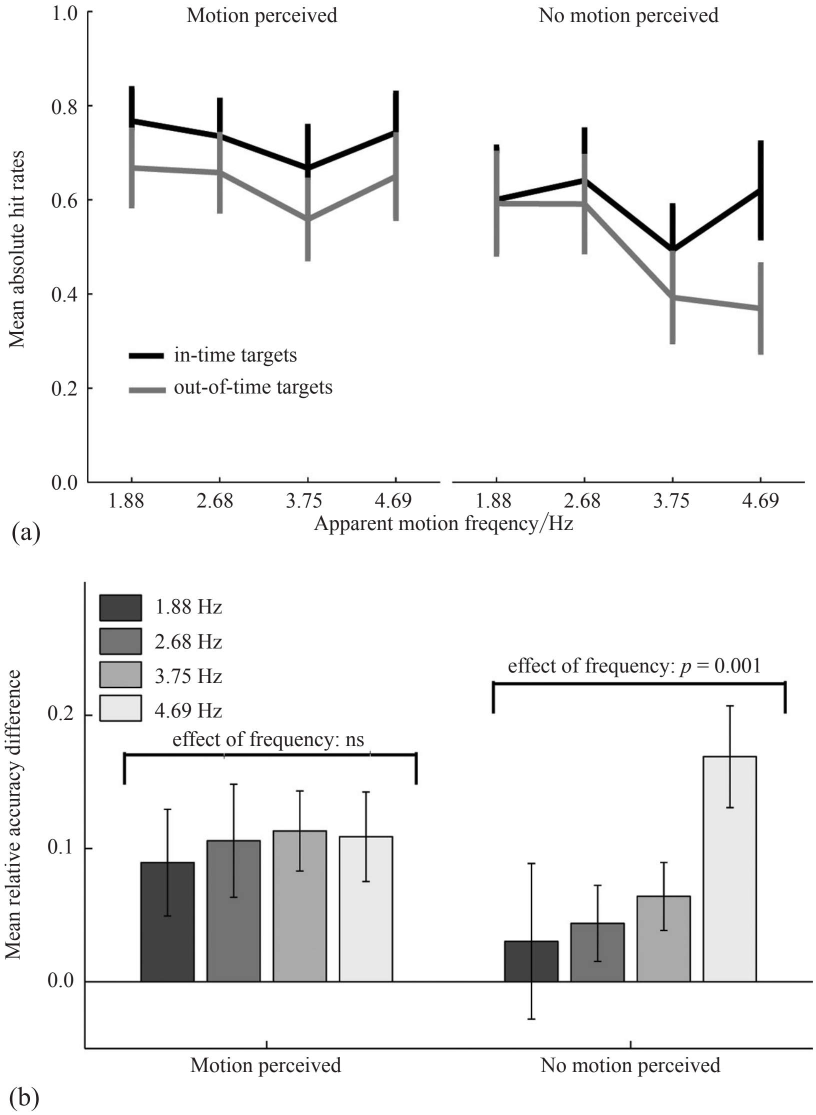

Figure 2. Experimental results. (a) Mean absolute detection accuracy (hit rates) for in-time and out-of-time targets at all four apparent motion frequencies when apparent motion was consciously perceived and when no apparent motion was perceived. (b) Mean relative accuracy differences between in-time and out-of-time targets. A positive value indicates that in-time targets were detected better than out-of-time targets. All error bars represent SEM.

The same effects are evident as interaction (target type × frequency) in the absolute detection rate data (motion perceived: $F_{3,42} = 0.15$, $p > 0.1$; motion not perceived: $F_{3,42} = 6.92$, $p = 0.001$).

Taken together, when subjects reported to have consciously perceived apparent motion, our predictive effect (in-time targets being better detected than out-of-time targets) worked well independently of apparent motion frequency. However, when no smooth apparent motion was perceived, the predictive effect varied with frequency: at slow apparent motion frequencies the predictive effect was weak, but grew stronger at fast apparent motion frequencies.

3 Discussion

Here we show that while prediction and conscious awareness of the predicted percept may coincide, a dissociation between both can be observed. Our results demonstrate that, when smooth illusory motion is perceived, the spatiotemporally specific prediction of a moving token on the apparent motion path works reliably. However, when illusory motion is not consciously perceived, prediction of motion-like regularity can nevertheless work at high apparent motion frequencies or fail at low apparent motion frequencies.

We suggest that at low apparent motion frequencies the temporal dynamics of the visual stimuli is so slow that, in case of no apparent motion perception, the flashing stimuli and the target are perceived as independent perceptual events and the motion prediction fails. That is, a new stable percept of flicker takes over and clears the motion prediction in between the inducing stimuli. At high apparent motion frequencies, temporal dynamics of the incoming sensory input are such that the predictive model is always well supported and it works reliably even when apparent motion is not consciously perceived. That is, predictions of motion-like regularity exist both with the percept of motion and with the percept of flicker. The latter case shows that motion prediction can work successfully without conscious awareness of the predicted motion percept. However, in the case when apparent motion is consciously perceived, the brain binds the flashing stimuli into a continuous motion prediction and our predictive effect is present irrespective of the temporal dynamics of the flashing stimuli. In this case, conscious perception helps prediction.

For the role of consciousness in prediction, this means that, at high apparent motion frequencies, targets are more likely to be perceived when they are presented in a predictable motion context, even if this context itself is not perceived as motion—as if the context provides an unconscious bias (ie like meta-contrast masking or some forms of unconscious semantic priming, eg Kouider, de Gardelle, Sackur, & Dupoux, 2010; Maus, Weigelt, Nijhawan, & Muckli, 2010). Whether the motion context itself is perceived as motion may depend on other factors: for example, access to the global workspace (Dehaene & Changeux, 2011). The perception of motion therefore does not seem to have an enhancing function at high temporal frequencies, as predictable targets are always favoured regardless of motion perception. At low temporal frequencies, however, the conscious percept of apparent motion has an enhancing function: it triggers a bias for predicted stimuli which is absent when flicker is perceived. That is, in cases when the incoming sensory input provides unreliable or ambiguous information, conscious awareness of the context can help the brain choose the internal model that is best predictive.

Our present findings suggest that the creation of the motion prediction and the creation of the conscious apparent motion percept may reflect different neural mechanisms in the brain. Other experiments have shown that predictions can be created and modulated flexibly even without consciousness (den Ouden, Friston, Daw, McIntosh, & Stephan, 2009; Kok, Brouwer, van Gerven, & de Lange, 2013; Wacongne et al., 2011). We suggest that motion area V5, in particular, and possibly higher motion areas in parietal cortex play an important role in binding the inducing stimuli to either smooth apparent motion or flicker and in mediating the prediction effect. In certain high-frequency circumstances these motion-like predictions might be induced even though they are not perceived as motion.

Several neuroimaging studies provided evidence for human motion complex V5/MT, intraparietal sulcus (IPS), and intraparietal lobule (IPL) responding stronger to apparent-motion-inducing stimuli than to simultaneously flickering flashes never inducing apparent motion (Claeys, Lindsey, De Schutter, & Orban, 2003; Goebel et al., 1998; Muckli et al., 2002). apparent motion stimulation induces a predictive internal model of motion in V5 and sends a predictive signal to V1 (Sterzer, Haynes, & Rees, 2006; Vetter et al., in press; Wibral, Bledowski, Kohler, Singer, & Muckli, 2009). In V1 an activation along the nonstimulated retinotopic location of the apparent motion trace can be observed, reflecting a neural correlate of the illusory motion token (Muckli et al., 2005; Sterzer et al., 2006; Wibral et al., 2009) and switching location according to the perception of the motion path (Muckli et al., 2005). During perceptual switches between smooth apparent motion and flicker, V5 is less activated during flicker than during apparent motion (Muckli et al., 2002; Sterzer, Russ, Preibisch, & Kleinschmidt, 2002).

Our present psychophysical study adds an important aspect here: even though V5 correlates with the perception of smooth apparent motion and creates a motion prediction, the motion prediction can work also during flicker, so presumably when V5 activity is reduced. Here it seems that at high apparent motion frequencies, recurrent loops between V5 and V1 operate an automatic motion detection process that creates the prediction independent of motion perception. Furthermore, our results are consistent with the possibility that the conscious percept of smooth apparent motion may not be solely created in V5, but also in other higher order motion areas responding to apparent motion—for example, IPL, the superior temporal sulcus (STS), the IPS, or posterior insula (PI; Claeys et al., 2003). These areas, in turn, are linked to frontoparietal areas involved in conscious perception (eg Dehaene & Changeux, 2011; Sterzer et al., 2002). That is, when apparent motion is perceived, these areas are active and may feed back to V5 (and possibly to V1) the presence of an illusory motion token, strengthening the prediction in V5. When only flicker is perceived, the feedback from these areas to V5 is weakened and the internal model in V5 needs strong feedforward input (fast frequencies) to create a successful prediction. While it may be the case that the internal predictive model is created exclusively by higher order motion areas, our results at fast frequencies suggest that the prediction can still work without conscious apparent motion perception, thus possibly solely via a recurrent V5–V1 loop.

It may also be relevant to note that higher order motion areas respond differently to different apparent motion frequencies: compared with flicker, IPL responds mostly to 7 Hz apparent motion, STS mostly to 2 Hz, and IPS and PI to both frequencies (Claeys et al., 2003). V5, however, is active during apparent motion irrespective of frequency (2, 2.5, and 7 Hz; Claeys et al., 2003; Muckli et al., 2002). For our results, this could mean that these areas exert differential influences on V5 and lower areas depending on apparent motion frequency—however, only during conscious apparent motion perception. Given that we observe frequency modulation in our results only during flicker, these neuroimaging findings do not directly explain our results. Further neuroimaging studies are needed to delineate exactly the influence of higher order motion areas on predictive processes in the presence and absence of conscious apparent motion perception. In sum, our results demonstrate that prediction and conscious awareness of the predicted percept can dissociate and furthermore highlight a potential evolutionary role for consciousness: the predictive power of brain processes can be enhanced by conscious perception.

4 Methods

Fifteen participants (eleven females, mean age = 24.4 years) with normal or corrected vision participated after signing informed consent. Refresh rate was 75 Hz (frame duration: 13.33 ms). Two apparent-motion-inducing white squares (2.5 deg visual angle, 14.8 deg vertical distance) were flashed for 5 frames (67 ms), each on a grey background in the right peripheral field (see figure 1 for stimulus size, distances, timings, and sequence). Interstimulus intervals (ISIs) between the two squares were either 15, 9, 5, or 3 frames, resulting in four different apparent motion frequencies: F1: 1.88 Hz, F2: 2.68 Hz, F3: 3.75 Hz, and F4: 4.69 Hz, respectively. To keep overall trial duration approximately the same, trials with slower frequencies contained fewer apparent motion cycles than trials with faster frequencies (4, 6, 8, and 10 cycles per trial for F1, F2, F3 and F4, respectively). This resulted in a trial duration of 2.13 s for F1, F3, and F4 and a trial duration of 2.24 s for F2. Targets (2 deg) were displayed for 1 frame in a randomly chosen apparent motion cycle in the middle of the trial. In 60% of the trials the target was displayed below the midline (target of interest), in 10% above the midline (catch trials, excluded from analysis), and in 30% there was no target. Half the targets appeared in time and half out of time with the illusory motion token. That is, in-time targets were displayed spatiotemporally congruent with a linearly moving token, and out-of-time targets were incongruent—that is, at the same time but at the wrong position (see also Schwiedrzik et al., 2007; Vetter et al., 2012; Vetter et al., in press, for an illustration of target timing across space). For the targets of interest, this meant that in-time targets were displayed at ISI frames 4, 3, 2, or 1 in upward apparent motion, and at ISI frames 12, 7, 4, or 3 in downward apparent motion for the four different apparent motion frequencies, respectively. Apparent motion direction, apparent motion frequency, target timing, and target position were pseudorandomised and counterbalanced within each run. A natural scene was displayed for 25 s after every 40 trials as a break and to counter apparent motion adaptation. Subjects performed a two-alternative forced-choice task on whether they saw the target, and whether they perceived apparent motion. Central fixation was monitored by eye-tracking. Subjects performed 800 trials in total, broken down into 4 runs of 200 trials each.

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