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The temporal dynamics of the perceptual consequences of action-effect prediction

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ABSTRACT

An essential aspect of voluntary action control is the ability to predict the perceptual effects of our actions. Although the influence of action-effect prediction on humans' behavior and perception is unequivocal, it remains unclear when action-effect prediction is generated by the brain. The present study investigates the dynamics of action effect anticipation by tracing the time course of its perceptual consequences. Participants completed an acquisition phase during which specific actions (left and right key-presses) were associated with specific visual effects (upward and downward dots motion). In the test phase they performed a 2 AFC identification task in which they were required to indicate whether the dots moved upward or downward. To isolate any effects of action-effect prediction on perception, participants were presented with congruent and incongruent dot motion in which the association participants learned in the previous acquisition phase was respected and violated, respectively. Crucially, to assess the temporal dynamics of action prediction, congruent and incongruent stimuli were presented at different intervals before or after action execution. We observed higher sensitivity (d') to motion discrimination in congruent vs. incongruent trials only when stimuli were presented from about 220 ms before the action to 280 ms after the action. The temporal dynamics of our effect suggest that action-effect prediction modulates perception at later stages of motor preparation.

1. Introduction

The ability to predict the perceptual effects of our actions is an essential aspect of action control (cf., Wolpert, 1997, see also Schmidt, 1975). The influence of action-effect prediction on human behavior and perception has been demonstrated in a large number of studies (for review see Hughes, Desantis, & Waszak, 2013; Shin, Proctor, & Capaldi, 2010; Waszak, Cardoso-Leite, & Hughes, 2012). For instance, it has been observed that predicted effects are perceived as less intense compared to unpredicted effects (e.g., Baess, Widmann, Roye, Schröger, & Jacobsen, 2009; Blakemore, Wolpert, & Frith, 1998; Cardoso-Leite, Mamassian, Schütz-Bosbach, & Waszak 2010; Roussel, Hughes, & Waszak, 2013). Recent studies explained this phenomenon in terms very similar to predictive coding. Namely, action preparation/execution results in the pre-activation of the sensory network that represent the sensory action-effect (see Kuhn, Seurinck, Fias, & Waszak, 2010; Roussel et al., 2013; SanMiguel, Widmann, Bendixen, Trujillo-Barreto, & Schröger, 2013;

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Waszak et al., 2012), as a consequence the neural response to incoming stimulation is smaller because sensory areas are pre-activated. Although the influence of action-effect prediction on human behavior and perception is unequivocal, it remains unclear when action-effect prediction is generated by the brain. The present study aimed at investigating this issue by tracing the temporal dynamics of both predicted and unpredicted perceptual consequences (see also Bays, Wolpert, & Flanagan, 2005; Ziessler & Nattkemper, 2011). In other words, we aimed at assessing which stage of motor preparation/execution modulates our perception of predicted action-effects. The question of whether the perceptual consequences of action-effect prediction are related to preparatory stages of motor processing or rather to the execution of the action is essential, as it helps in the understanding of the function of action-effect anticipation (cf., Ziessler & Nattkemper, 2011).

On the one side, according to the schema theory (Schmidt, 1975) action-effect prediction is necessary to monitor action execution. Accordingly, effect anticipation can be used for quality control and error handling. For instance, it has been shown that action-effect anticipation is necessary to maintain movement stability. The presence of large temporal delays between the execution of rapid movements and their sensory consequences results in instability of the behavior. Internal prediction of action sensory consequences might be used before the true sensory reafferences are available, thereby ensuring the correct execution of a sequence of actions (cf., Wolpert, 1997). Thus, predicted effects can be used for an internal test of the motor programme in advance of its execution (Schmidt, 1975). From this perspective effect anticipation could occur at later stages of motor preparation or during action execution. That is, we should observe a perceptual modulation of predicted effects during later stages of action preparation.

However, according to the ideomotor principle of action control the anticipation of action-effects is even instrumental to the selection of the right action meant to achieve a given goal (cf., Harless, 1861; James, 1890; Lotze, 1852; Shin et al., 2010). The ideomotor theory claims that performing an action results in a bidirectional association between the action's motor code and the sensory effects the action produces. Once acquired, these associations can be used to select an action by anticipating or internally activating their perceptual consequences (e.g., Elsner & Hommel, 2001; Herwig, Prinz, & Waszak, 2007; Prinz, 1997). A strong version of this theory assumes, thus, that effect anticipation is an integral part of action selection (e.g., James, 1890; Prinz, 1997). Effect anticipation should therefore necessarily take place at early stages of motor preparation. Accordingly, we reasoned that a difference in the perception of predicted vs. unpredicted effect should appear during early stages of action preparation.

Finally, action-effect prediction might not only contribute to sensorimotor control and action selection, but also to the emergence of people's belief of authorship (Blakemore, Wolpert, & Frith, 2002), since it would help labeling movements and correctly predicted sensory consequences as generated by oneself (e.g., Sato & Yasuda, 2005): a match between predicted and actual sensory events might lead the system to label sensory events as self-generated. Instead, a mismatch between what is expected and what actually happens, might lead an individual to consider the event as externally triggered (e.g., Blakemore et al., 2002; Wolpert, 1997). Whether early/late motor preparation execution is involved in the generation of action-effect anticipations would therefore also shed further light on the understanding of processes involved in the distinction between self and externally generated events.

In the present study, participants completed an acquisition phase during which specific actions (left and right key-presses) were associated with specific visual effects (dots moving upward or downward). In the test phase they completed a 2 AFC identification task in which they were required to indicate whether the dots moved upward or downward. To isolate any effects of action-effect prediction, participants were presented with congruent and incongruent dot motion in which the association they learned in the previous acquisition phase was respected or violated, respectively. Crucially, to assess the temporal dynamics of action prediction, congruent and incongruent stimuli were presented at different time points not only after but also before action execution.

We observed higher sensitivity (d') to motion discrimination in congruent vs. incongruent trials only when stimuli were presented from about 220 ms before the action to 280 ms after the action. The temporal dynamics of our effect suggests that the perceptual modulation of action-effect prediction occurs during motor preparation. As we will discuss below, our results also corroborate the predictions of the pre-activation model concerning the influence of action-effect anticipation on identification d'.

2. Materials and methods

2.1. Materials

Stimulus presentation and data acquisition were conducted using the psychophysics Toolbox (Brainard, 1997; Pelli, 1997) for Matlab 7.5.0 running on a PC computer connected to a 19-in. 85 Hz CRT monitor. Auditory stimuli were presented via a pair of headphones.

2.2. Participants

Sixteen volunteers (average age = 26.34 years, *SD* = 5.42 years) participated in the experiment for an allowance of € 10/h. All had normal or corrected-to-normal vision and hearing and were naïve as to the hypothesis under investigation. They all gave written informed consent.

Participants completed 40 acquisition and 40 test phases presented in an ABAB order.

2.3. Acquisition phases

The aim of the acquisition phases was to build action-effect associations. Participants were presented with a Random Dot Kinematogram (RDK) in which 100 dots (dots size: 0.107 deg) were displayed within a circular aperture