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Anticipating action effects recruits audiovisual movement representations in the ventral premotor cortex

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ABSTRACT

When table tennis players anticipate the course of the ball while preparing their motor responses, they not only observe their opponents striking the ball but also listen to events such as the sound of racket–ball contact. Because visual stimuli can be detected more easily when accompanied by a sound, we assumed that complementary sensory audiovisual information would influence the anticipation of biological motion, especially when the racket–ball contact is not presented visually, but has to be inferred from continuous movement kinematics and an abrupt sound. Twenty-six observers were examined with fMRI while watching point-light displays (PLDs) of an opposing table tennis player. Their task was to anticipate the resultant ball flight. The sound was presented complementary to the veracious event or at a deviant time point in its kinematics.

Results showed that participants performed best in the complementary condition. Using a region-of-interest approach, fMRI data showed that complementary audiovisual stimulation elicited higher activation in the left temporo-occipital middle temporal gyrus (MTGto), the left primary motor cortex, and the right anterior intraparietal sulcus (aIPS). Both hemispheres also revealed higher activation in the ventral premotor cortex (vPMC) and the pars opercularis of the inferior frontal gyrus (BA 44). Ranking the behavioral effect of complementary versus conflicting audiovisual information over participants revealed an association between the complementary information and higher activation in the right vPMC. We conclude that the recruitment of movement representations in the auditory and visual modalities in the vPMC can be influenced by task-relevant cross-modal audiovisual interaction.

1. Introduction

Anticipating what others are going to do is an everyday phenomenon, and when it comes to many sports, anticipating an opponent's action is especially important for successful performance. For example, if table tennis players observing their opponents' serve are to have any chance of making a successful return, they must prepare their own motor responses to match the anticipated direction of ball flight. Anticipation in this sense includes paying attention to behaviorally relevant stimuli and deciding on an appropriate reaction. Anticipation performance has been found to be particularly important when athletes have to act under extreme time pressure (Williams, Ford, Eccles, & Ward, 2011; Wolpert, Doya, & Kawato, 2003). In such situations, it is possible to isolate and study reaction-oriented perception. When the goal is to prepare a response stroke the observer actively samples the scene and seeks the sensory consequences with an "active inference" (Friston, Daunizeau, & Kiebel, 2009) or "active sensing" (Schroeder, Wilson, Radman, Scharfman, & Lakatos, 2010). In hierarchical predictive coding approaches of the brain (e.g., Friston et al., 2009) top-down predictions are matched with the perceived sensory signals in order to minimize error, thereby the world is represented in the brain via efficient models. While both perception and action minimize this prediction error, action plays a special role by minimizing the "surprise", i.e. the mismatch between the perceived sensory signals and those predicted (Friston, 2013). That is, perception selects the sensory input, action

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changes the input. And movement representations inform about the probable consequences of actions. Actions of others known to an observer offer a clear benefit for anticipation, because their sensory consequences can be estimated by simulating the movements. In the literature, the simulation of observed actions has been discussed as one possible mechanism underlying anticipation (Knoblich & Flach, 2001; Wolpert, Ghahramani, & Jordan, 1995; Wolpert et al., 2003). Simulation theories propose that observed movements correlate with a neural representation in the brain. This representation is then compared with the observer's own representations of own movements and goals (Jeannerod, 2001; Schubotz, 2007; Wilson & Knoblich, 2005; Wolpert & Flanagan, 2001; Zentgraf, Munzert, Bischoff, & Newman-Norlund, 2011). When a task involves more than neutral observation – that is, when observers are trying to achieve certain goals and are preparing to interact with their environment – they are likely to use this simulation process for anticipation. Hence, simulation is particularly interesting for reaction-oriented perception, and we should be able to enhance our knowledge about anticipation by manipulating which sensory information is processed. Because the integration of motor and sensory aspects of movements during simulation seems to be essential for anticipation (for reviews, see Shmuelof & Zohary, 2005; Zentgraf et al., 2011), one can also ask how far simulation involves representations in more than one sensory modality, that is, multisensory representations. When events have to be perceived with high temporal precision, critical information can be gained from the auditory sensory modality in interaction with vision (see, for a review, Chen & Vroomen, 2013; Murray & Spierer, 2009). Hence, anticipating a goal-directed action in order to prepare an appropriate reaction may be susceptible to cross-modal effects.

In naturalistic settings, observers do not just rely on visual information but may also use other perceptual modalities, notably acoustic information. Vroomen and De Gelder (2000) found that subjects could detect targets in a rapidly changing pattern far better when a sound was presented with the target configuration. This advantage of auditory stimulation was due purely to the time information and not to any spatial alignment. Van der Burg, Olivers, Bronkhorst, and Theeuwes (2008) presented a crowded display of small line segments that changed color continuously between red and green. When the color changes in the target stimulus were accompanied by a spatially nonspecific sound, the search time decreased. The authors proposed that audiovisual integration captures attention during the processing of competing visual stimuli. To investigate the influence of multisensory integration on moving stimuli, Staufenbiel, van der Lubbe, and Talsma (2011) presented randomly moving dots, one of which changed direction in some trials. The motion direction change was accompanied by a sound, whereas in trials without direction change, a noninformative sound was presented. Participants were better at detecting direction changes and could keep track of a higher number of visual stimuli. Staufenbiel et al. (2011) stressed that the sound was presented after movement initiation of the target, making it unlikely for the sound to be just a warning signal. They also suggested that the auditory stimulus used to mark timing information needs to be a salient and abrupt event (Staufenbiel et al., 2011).

The present study aims to extend these findings to biological motion by investigating the influence of multisensory integration on brain activation during the anticipation of action effects. We wanted to find out more about the recruitment of multisensory (audiovisual) representations during reaction-oriented anticipation. Actively sensing the relevant events and the relevant modalities benefits perceptual anticipation.

A number of brain areas have been found to be involved in the multisensory processing of actions. Caspers, Zilles, Laird, and Eickhoff (2010) focused on the action observation network (AON) in a meta-analysis of fMRI studies. They reported that the AON encompasses the lateral temporo-occipital cortex as well as parietal areas (including the intraparietal sulcus) and premotor areas. In the ventral premotor cortex (vPMC) of the monkey, neurons of the so-called mirror-neuron system (MNS) were found to be sensitive to visual and auditory stimulation in action recognition and action understanding tasks (Keysers et al., 2003; Kohler et al., 2002). In human vPMC, audiovisual information has been shown to facilitate action understanding more than unimodal stimulation (Kaplan & Iacoboni, 2007). Alaerts, Swinnen, and Wenderoth (2009) suggested that higher responses to audiovisual input in the human primary motor cortex are caused by shared modality-dependent action representations. James, Van Der Klok, Stevenson, and James (2011) focused on the recognition of object-directed action while information was being presented in different sensory modalities. They found activation for auditory and visual recognition bilaterally at the temporo-occipital junction, in the left superior temporal sulcus (STS), and bilaterally in the intraparietal sulcus (IPS). Although MNS neurons have not been found in the STS itself, areas in the sulcus show sensitivity to biological motion, and many fiber connections from the STS also project to the inferior parietal lobe (Kilner & Frith, 2007). According to this literature, the regions of interest (ROI) when investigating influences of complementary audiovisual information on the anticipation of action effects, are the primary auditory and motor cortices along with the STS, the MTG, the aIPS, the vPMC, and the inferior frontal gyrus (IFG).

The rationale underlying the present study assumes that anticipation-relevant information is integrated across two distinct sensory modalities in order to provide one single overall percept. Depending on the salience of one modality – that is, on the degree of noise – the second modality may substitute information that was lost in the first modality. In table tennis, for example, some characteristics of a striking movement such as its speed and timing may be estimated from the sound occurring at the moment of racket–ball contact (RBC). Hence, information from both modalities is relevant for players preparing a reaction to their opponent's serve. To isolate this information in the present experimental setting, we reduced the visual kinematic information on the moving opponent to point-light displays (PLDs) to remove information in the visual modality. These PLDs did not include markers of the racket and the ball. This was then combined with the presentation of an informative auditory cue to the RBC. The racket and the ball were occluded, which means the auditory cue was the only sensory information on the RBC. Without sound, observers could infer the RBC based only on their own movement representations without being able to draw on precise sensory information in the display. When both sensory modalities contributed information, they would be able to compare both the sensory and the movement representations. Only audiovisual stimuli around the RBC elicit anticipation based on audio and visual representations. A sound at the movement beginning is not perceived as originating from the RBC half a second later.

The experimental setting situated participants as players in a table tennis game, who observed the opposing player and anticipated the direction of the ball flight to prepare their response. We examined the behavioral effects of complementary and conflicting audiovisual information on perceptual performance (correct responses) and which brain areas were activated differentially during anticipation. Our main hypothesis was, that complementary audiovisual stimulation – marking the veracious RBC – would result in higher brain activation in the path from primary sensory areas over (other) sensory integration areas to motor and premotor areas. Especially, multisensory representations in premotor areas were expected to be used for anticipation in all conditions, but more so when audiovisual stimulation was complementary. Complementary audiovisual stimuli inform about one