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Allocentric information is used for memory-guided reaching in depth: A virtual reality study

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A B S T R A C T

Previous research has demonstrated that humans use allocentric information when reaching to remembered visual targets, but most of the studies are limited to 2D space. Here, we study allocentric coding of memorized reach targets in 3D virtual reality. In particular, we investigated the use of allocentric information for memory-guided reaching in depth and the role of binocular and monocular (object size) depth cues for coding object locations in 3D space. To this end, we presented a scene with objects on a table which were located at different distances from the observer and served as reach targets or allocentric cues. After free visual exploration of this scene and a short delay the scene reappeared, but with one object missing (=reach target). In addition, the remaining objects were shifted horizontally or in depth. When objects were shifted in depth, we also independently manipulated object size by either magnifying or reducing their size. After the scene vanished, participants reached to the remembered target location on the blank table. Reaching endpoints deviated systematically in the direction of object shifts, similar to our previous results from 2D presentations. This deviation was stronger for object shifts in depth than in the horizontal plane and independent of observer-target-distance. Reaching endpoints systematically varied with changes in object size. Our results suggest that allocentric information is used for coding targets for memory-guided reaching in depth. Thereby, retinal disparity and vergence as well as object size provide important binocular and monocular depth cues.

1. Introduction

The human brain makes use of egocentric (relative to the observer) and allocentric (relative to objects in the environment) reference frames (Battaglia-Mayer, Caminiti, Lacquianiti, & Zago, 2003; Colby, 1998; Klatzky, 1998) to encode object locations for action in the environment. Previous studies demonstrated that egocentric, and in particular gaze-centered, reference frames are predominantly utilized when planning and executing reaching movements toward the remembered location of a visual target (e.g. Cohen & Anderson, 2002; Fiehler, Schütz, & Henriques, 2011; Thompson & Henriques, 2011). However, other studies also revealed evidence for the use of allocentric reference frames for memory-guided reaching (e.g. Diedrichsen, Werner, Schmidt, & Trommershäuser, 2004; Krigolson, Clark, Heath, & Binsted, 2007; Krigolson & Heath, 2004; Obhi & Goodale, 2005) arguing for a combined use of both classes of coding schemes (Byrne & Crawford, 2010; Schütz, Henriques, & Fiehler, 2013, 2015).

Since most of the previous work used rather artificial stimuli like dots and bars, recent work aimed to increase ecological validity of the outcomes by using more naturalistic stimuli (Camors, Jouffrais, Cottereau, & Durand, 2015; Fiehler, Wolf, Klinghammer, & Blohm, 2014; Klinghammer, Blohm, & Fiehler, 2015). For example, in a previous study we presented computer generated images of a breakfast table on a computer screen and asked participants to memorize the locations of six objects on the table (Klinghammer et al., 2015). Then, the whole scene vanished and after a brief delay the scene reappeared for 1000 ms with one of the objects missing and the remaining objects shifted either to the left or to the right. Participants were instructed to reach to the location of the missing object on a grey screen while keeping gaze fixed. Reaching endpoints systematically deviated into the direction of the shifts of the remaining objects suggesting that allocentric information

Abbreviations: IRE, Induced Roelofs Effect; HMD, head mounted display; MERE, maximal expected reaching error.

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was used to encode the location of the reach target which was then integrated into the reach plan. In the present study, we aim to extend the outcomes of our preceding work from 2D to 3D space by transferring our established paradigm to virtual reality. This allows us to examine the use of allocentric information for memory-guided reaching not only in the horizontal axis but also in depth in real-world-like situations and to determine the role of binocular and monocular (i.e., object size) depth cues for allocentric encoding of memorized object locations when reaching in depth.

So far, we presented 2D stimuli and shifted objects in the left-right (horizontal) plane (Fiehler et al., 2014; Klinghammer et al., 2015). But how do object shifts in depth affect memory-guided reaching movements? It has been demonstrated that delayed pointing to a single target in the dark leads to pointing errors in the horizontal plane that are uncorrelated with pointing errors in the depth plane arguing for two independent subsystems for retaining target locations for action (Chieffi & Allport, 1997). Moreover, research on the Induced Roelofs Effect (IRE) (Coello, Richaud, Magne, & Rossetti, 2003), which describes the misestimation of the position of a target dot placed within a frame into the direction of the closest edge of this frame, shows that the orientation of the surrounding frame influences perception and action differently. While for a horizontally oriented frame the misestimation of the target dot was only found for perceptual judgements, for a frame orientation in depth this misestimation was also observed for memory-guided reaching movements. This suggests that the reach system is especially sensitive to contextual information, when the processing of depth cues is emphasized. By applying a similar IRE paradigm, Neely, Heath, and Binsted (2008) in contrast showed that reaching endpoints were influenced by both orientations of the frame. The authors concluded that one unitary visual system integrates allocentric and egocentric information for both orientation and distance of reaching movements. Thus, it is still unclear whether reaching targets are similarly or differently affected by allocentric information in the distance versus the directional axis. Here, we investigate the use of allocentric information for memory-guided reaching in the horizontal and the depth plane in a more naturalistic environment.

To perceive depth in a visual environment without self-motion, the human brain makes use of monocular (e.g., occlusion, height in the visual field, relative size) and binocular (e.g., binocular disparity, accommodation, vergence) depth cues. Depending on the distance between the observer and object locations in depth, the multiple depth cues are weighted and combined in different ways (Armbrüster, Wolter, Kuhlen, Spijkers, & Fimm, 2008; Cutting, 1997; Knill, 2005; Landy, Maloney, Johnston, & Young, 1995). One strong binocular depth cue for estimating objects' distances in depth is binocular disparity (Bingham, Bradley, Bailey, & Vinner, 2001). A virtual-reality-device such as the Oculus Rift DK2 (Oculus VR, LLC, Menlo Park, CA, USA) makes use of binocular disparity by presenting a slightly shifted perspective of the same scene to the two eyes, mimicking real world perception. In that sense, vergence can also be used providing a reliable depth cue within reaching space (Tresilian, Mon-Williams, & Kelly, 1999; Viguier, Clément, & Trotter, 2001). However, especially actions like prehension of objects need accurate metric depth information which cannot be provided by binocular cues alone (Hibbard & Bradshaw, 2003), but require the use of additional monocular depth cues for accurate depth perception (Bruno & Cutting, 1988; Magne & Coello, 2002).

For example, in a virtual environment study by Naceri, Chellali, and Hoinville (2011), a sphere located in different depths in front of the participants was used as pointing target. In one condition, the absolute size of the sphere was manipulated in a way that irrespective of its actual location in depth, the angular size (i.e., the retinal size) was kept constant. The results demonstrated that the absolute size manipulation influenced depth perception in a subgroup of participants. Regardless of the actual depth position of the sphere, they pointed to the same position as indicated by the constant angular size of the sphere. Based on this finding, the authors concluded that the object size was used as the main depth cue for pointing. The remaining participants were not influenced by the size manipulation and pointed to the correct location of the sphere according to its position in depth. This suggests that in this group of participants vergence was used as the dominant depth cue. In a later study, they again found that around half of the participants relied on object size and misjudged target depth when they verbally estimated target distances in a virtual reality, whereas the other half made use of vergence and correctly reported object distances (Naceri, Moscatelli, & Chellali, 2015). Hence, object size provides one important depth cue which can influence the perceived location of targets for action.

In this study, we aimed to answer two major questions. First, in order to test for potential differences when reaching to objects in virtual reality, we wanted to replicate our previous findings from a 2D paradigm (Klinghammer et al., 2015) in 3D virtual reality. Second, with the possibility of extending space to the third dimension, we wanted to know whether and how allocentric information is utilized for encoding the location of targets in depth for memory-guided reaching and how this is influenced by binocular and monocular (object size) depth cues.

For this purpose, we conducted two experiments. In experiment 1, we transferred our paradigm of Klinghammer et al. (2015) to 3D virtual reality and shifted objects on a breakfast table horizontally before reaching to the remembered location of a visual target. Moreover, we placed objects at three different distances from the observer to test whether 2D effects were consistent across different depth planes. In experiment 2, we used the same paradigm but this time shifted objects in depth and additionally manipulated the depth plane and the size of the objects serving as allocentric cues.

2. Experiment 1

2.1. Introduction

In order to extend the findings from our previous studies (Fiehler et al., 2014; Klinghammer et al., 2015) to a more realistic environment, we aimed to replicate the results from the 2D paradigm in 3D virtual reality. Participants wore a head-mounted display and had to encode the location of several virtual objects on a virtual table before performing a memory-guided reaching movement to the location of a remembered target object. Between scene viewing and reaching, the remaining objects were shifted horizontally. Moreover, object clusters were placed in three different distances to the observer. Based on our previous findings using 2D images (Klinghammer et al., 2015), we expect a similar systematic deviation of reaching endpoints in the direction of lateral object shifts. Since coding of reach targets in the horizontal plane should be independent from coding of reach targets in the sagittal plane (Chieffi & Allport, 1997), we expect lateral deviations of reaching endpoints to be independent of the observer-target distance.

2.2. Methods

2.2.1. Participants

Thirteen volunteers participated in the experiment (6 female), aged 19–31 years (mean 23.7 ± SD 3.9 years). All had normal or corrected-to-normal vision and intact stereo vision as determined by the Graded circle test (part of the Stereo fly test, STEREO OPTI-