Allocentric coding: Spatial range and combination rules

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ABSTRACT

When a visual target is presented with neighboring landmarks, its location can be determined both relative to the self (egocentric coding) and relative to these landmarks (allocentric coding). In the present study, we investigated (1) how allocentric coding depends on the distance between the targets and their surrounding landmarks (*i.e.* the spatial range) and (2) how allocentric and egocentric coding interact with each other across targets-landmarks distances (*i.e.* the combination rules). Subjects performed a memory-based pointing task toward previously gazed targets briefly superimposed (200 ms) on background images of cluttered city landscapes. A variable portion of the images was occluded in order to control the distance between the targets and the closest potential landmarks within those images. The pointing responses were performed after large saccades and the reappearance of the images at their initial location. However, in some trials, the images' elements were slightly shifted (±3°) in order to introduce a subliminal conflict between the allocentric and egocentric reference frames. The influence of allocentric coding in the pointing responses was found to decrease with increasing target-landmarks distances, although it remained significant even at the largest distances ($\geqslant 10°$). Interestingly, both the decreasing influence of allocentric coding and the concomitant increase in pointing responses variability were well captured by a Bayesian model in which the weighted combination of allocentric and egocentric cues is governed by a coupling prior.

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1. Introduction

Being able to form, maintain and update representations of objects locations in surrounding space is mandatory for flexible and adaptive behaviors. Depending on the spatial task at hand and on the properties of the surrounding space, human subjects have been shown to rely on two non-mutually exclusive types of spatial representations: (1) egocentric representations, in which spatial locations are encoded with respect to the self and (2) allocentric representations, in which locations are encoded with respect to external landmarks (Burgess, 2006; Colby, 1998; Tatler & Land, 2011).

Converging lines of evidences indicate that subjects rely on egocentric, gaze-centered, representations when pointing/reaching toward the memorized locations of visual targets that were presented within neutral surrounds, *i.e.* in the absence of external landmarks (Cohen & Andersen, 2002; Lacquaniti & Caminiti, 1998; Medendorp et al., 2008; Thompson & Henriques, 2011).

However, it is also been shown that when visual or cognitive landmarks are provided with the visual targets, these allocentric cues contributes to the mental representation of the targets location (Barry, Bloomberg, & Huebner, 1997; Carrozzo et al., 2002; Diedrichsen et al., 2004; Krigolson & Heath, 2004; Lemay, Bertram, & Stelmach, 2004a; Obhi & Goodale, 2005). Although some of the earliest studies have claimed that allocentric representations dominate and can even extinguish egocentric representations in the context of memory-based actions (Hay & Redon, 2006; Lemay, Bertram, & Stelmach, 2004a; Sheth & Shimojo, 2004), more recent studies rather support the idea of a weighted combination of these two types of spatial representation before action execution (Byrne, Cappadocia, & Crawford, 2010), with the weights being governed, at least partially, by the respective reliability of these two types of cues (Byrne & Crawford, 2010; Byrne & Henriques, 2013).

Cue reliability refers to the consistency of the representations derived from that cue alone, and is generally inferred from the reproducibility (the inverse of the variance) of the behavioral responses produced when only that cue is available (Battaglia, Jacobs, & Aslin, 2003; Ernst, 2006; Ernst & Banks, 2002; Girshick

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& Banks, 2009; Knill, 2007; Knill & Saunders, 2003; Körding et al., 2007; Landy et al., 1995; Young, Landy, & Maloney, 1993). Among the factors affecting the relative reliability (or weight) of allocentric versus egocentric cues, the importance of the temporal delay between targets/landmarks presentation and action execution has been repeatedly emphasized: a greater delay increases the weight allocated to allocentric cues, while decreasing the weight of egocentric cues (Carrozzo et al., 2002; Chen, Byrne, & Crawford, 2011; Hay & Redon, 2006; Obhi & Goodale, 2005; Sheth & Shimojo, 2004; but see Schütz, Henriques, & Fiehler, 2013, for an instance of constant allocentric/egocentric weights across time delays). In their majority, these observations are reminiscent to those reported for actions directed toward targets embedded in illusory visual contexts. Landmarks producing illusory biases in the targets' perceived size or position have been shown to exert a stronger influence on delayed actions than on those initiated during, or immediately after, the presentation of the illusory context (Bridgeman, Peery, & Anand, 1997; Gentilucci et al., 1996; Goodale, Westwood, & Milner, 2004; Hu & Goodale, 2000; Rossetti, 1998).

Other factors influencing the relative weight of allocentric and egocentric cues have been identified, such as the specificities in the task demand (Bridgeman, Peery, & Anand, 1997), the intrinsic stability (Byrne & Crawford, 2010) and predictability (Neely et al., 2008) of the allocentric landmarks, or the age of the subjects (Lemay, Bertram, & Stelmach, 2004b; Lemay & Proteau, 2003).

Surprisingly, another potentially important factor has received little interest: the spatial distance between the visual targets and their surrounding landmarks. Intuitively, it seems reasonable to assume that increasing the targets to landmarks distance should impair the precision to encode targets location relative to the surrounding landmarks. To our knowledge, only Krigolson and colleagues (2007) have addressed this question in a direct manner with a memory guided reaching task in which the landmarks occupied proximal (∼4°), medial (∼6°) or distal (∼8°) locations with respect to the visual targets during the memory encoding phase. They found that although proximal and medial landmarks had a beneficial effect regarding the reliability of the pointing responses (*i.e.* less dispersion in the pointing responses), the distal landmarks had no noticeable influence. This result suggests that allocentric coding is restricted to objects that are relatively close to each other (*i.e.* less than 8° apart in that particular experiment). The idea of a limited spatial range of allocentric coding is reinforced by studies (Diedrichsen et al., 2004; Schmidt, Werner, & Diedrichsen, 2003) showing that even when several landmarks are located within a few degrees apart from a target, only the closest one induces distortions in reaching end-points. An apparently related finding has been recently provided (Fiehler et al., 2014) with pictures of natural scenes in which both the targets and landmarks depicted real world objects. The proximal landmarks were found to influence the pointing responses while the distal ones did not. However, only the proximal landmarks were task-relevant in that previous study so it is unclear whether these proximal landmarks were more efficient because they were closer or because more attention was paid to them. A recent follow-up study from the same group supports this second hypothesis (Klinghammer et al., 2014).

It is important to note that the vast majority of the above-mentioned studies have relied on well controlled but highly artificial setups in which landmarks were isolated point-like objects, simple geometrical shapes or grid-like patterns. Even the last mentioned study (Fiehler et al., 2014) used relatively simple breakfast scenes, with a restricted number of visual objects on a table, and subjects could take as much time as needed to explore those scenes. Thus, the extent to which the accumulated knowledge can be generalized to more complex ecological situations remains largely unaddressed. For instance, does allocentric coding occur when landmarks are not provided in a neutral surround, or in relatively simple environments but must be extracted from short glimpses to cluttered visual scenes, such as those encountered when walking in crowded city streets? If allocentric coding does occur in more complex ecological conditions, is its spatial range more restricted than with artificial landmarks (Krigolson et al., 2007), and how does it combine with egocentric coding (Byrne & Crawford, 2010)? These questions on the spatial range and combination rules of allocentric coding are addressed in the present study.

We asked human subjects to perform a memory-based laser-pointing task toward previously gazed targets, which were briefly superimposed on background images of cluttered city landscapes. The presentation duration of both the targets and images was 200 ms, which is close to the average fixation time between two successive saccades during the exploration of natural visual scenes (Henderson, 2003; Martinez-Conde, Macknik, & Hubel, 2004; Rayner, 1998). Masks centered on the targets covered variable portions of the images in order to control the distance between the targets and the closest potential landmarks that are extracted from those images. After the memory encoding phase, subjects were required to perform a large saccade (25°) during total occlusion of the background images, which reappeared prior to the pointing response. The images reappeared at the same location but the content was, in some trials, slightly shifted (±3°) to the right or to the left side in order to introduce a subliminal conflict between the allocentric and egocentric reference frames. In the main experiment, subjects received the instruction to provide an allocentric-based judgment, *i.e.* to indicate where the fixation target was located within the picture, but they could rely on both allocentric and egocentric cues (either congruent or slightly incongruent) to perform the task. In additional control experiments, they were required to perform the same task in conditions where only the allocentric or egocentric cues were available. Such approach, in which cues are tested both separately and together, has already proven to be useful for inferring the cue combination rules in other contexts (Battaglia, Jacobs, & Aslin, 2003; Ernst, 2006; Ernst & Banks, 2002; Girshick & Banks, 2009; Knill, 2007; Knill & Saunders, 2003; Körding et al., 2007; Landy et al., 1995; Young, Landy, & Maloney, 1993).

The first main finding of the present study is that allocentric coding is functional in complex ecological conditions, *i.e.* when potential landmarks are seen briefly and must be extracted from cluttered visual scenes. This result still holds when the closest potential landmarks are 10° away from the target. The second main finding is that although subjects are required to produce allocentric-based spatial judgments, they rely on both allocentric and egocentric cues. Experimental results are well-captured by a Bayesian model in which the combination of allocentric and egocentric cues is governed both by their respective reliability and by a coupling prior (Bresciani, Dammeier, & Ernst, 2006; Ernst, 2006).

2. Material and methods

2.1. Participants

Ten subjects (6 males and 4 females) performed the experiment. All of them were university students (24.4 ± 4.9 years old) and had normal or corrected to normal vision. They provided written informed consent before participating in the study and received a monetary reward (20 euros) at the end of the experiment. This study was approved by the local ethic committee (CLERIT, n° 2014-06-06-6) based notably on its compliance with the Helsinki Declaration and its newest (2013) amendments.