



The coding and updating of visuospatial memory for goal-directed reaching and pointing

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ABSTRACT

In this review we discuss evidence from psychophysical, electrophysiological, and neuroimaging studies that demonstrates the updating of remembered visual space in a reference frame that is centred on the eye. We then extend these findings by discussing recent work from our lab. Specifically, we address eye-centred updating of visuospatial memory for arm movements following different types of eye movements, the role of retinal versus extraretinal information in such spatial updating, and the use of allocentric versus egocentric information in coding multiple targets. We provide a conceptual model to explain the relationships among these findings.

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1. Introduction

We move our eyes 4–5 times every second, resulting in a continuously changing stream of visual information, yet we still perceive the world to be stable. Perceived stability of the world is important because it allows us to function – a continuously shifting visual world would make interaction with the environment impossible, since the spatial locations of objects in our environment are behaviourally relevant both for interacting with objects and avoiding obstacles. While this can be explained by reference frame conversions (i.e., converting visual information to a stable body-centred reference frame, such as one fixed to the head or arm), the stability of visual information regarding the locations of distal objects (i.e., those not in contact with our bodies), is more likely related to the continuous updating, or remapping, of visual space. This review will present and discuss evidence that suggests that the updating of remembered visual space occurs in a reference frame that is centred on the eye.

2. Behavioural evidence of eye-centred spatial updating

Remembered locations of pointing targets have been shown to be remapped following an intervening saccade (Henriques, Klier, Smith, Lowy, & Crawford, 1998). When subjects moved their eyes

after briefly foveating a target before pointing to its remembered location, they overestimated the location of the remembered target relative to gaze. That is, when the eyes are repositioned to the right of a remembered target location, there is a leftward pointing error (and *vice versa*). This pattern of pointing error is consistent with those errors produced when pointing to targets that are only ever peripherally viewed (Bock, 1986). Since subjects showed the same pattern of errors when they foveated a target then looked away (as in Henriques et al. (1998)), as they did when pointing to a remembered target seen only peripherally – known as the retinal magnification effect – (as in Bock (1986)), it seems that remembered target locations are stored and updated in an eye-centred reference frame – the foveated target is remapped to the retinal periphery when the eyes move away. Other gaze-independent models (like one fixed to the head) cannot explain why a subsequent movement of the eyes following foveation (i.e., after the reference frame conversion) would lead to systematic reaching errors that are exclusively dependent on the location of the remembered target relative to gaze. Thus, these results suggest that these target locations in eye-centred coordinates are not converted to a muscle-based frame (e.g., one centred on the arm or on the hand), at least until the decision is made to generate an action toward that target (i.e., the Conversion on Demand Model, Henriques et al., 1998).

The updating of visuospatial memory relative to eye direction has also been demonstrated for a variety of different task parameters and experimental setups. These include the updating of remembered space in eye-centred coordinates for: near and far visual targets (Medendorp & Crawford, 2002; Van Pelt & Medendorp,

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2008); both explicit (distinct) and implicit (implied by the convergence point of a full field motion pattern) visual targets (Poljac & van den Berg, 2003); angular distances of the target relative to gaze produced by translating the entire body (Van Pelt & Medendorp, 2007); changing starting positions of both the seen and unseen hand (Beurze, Van Pelt, & Medendorp, 2006); multiple reaches to the same remembered target site with an intervening eye movement between reaches (Sorrento & Henriques, 2008); auditory (Pouget, Ducom, Torri, & Bavelier, 2002) and proprioceptive pointing targets (Blangero et al., 2007; Jones, Cressman, & Henriques, 2009; Pouget et al., 2002); and when judging the relative location of remembered visual and proprioceptive stimuli relative to the hand (Fiehler, Rosler, & Henriques, 2010). These studies indicate that not only are visual targets updated in an eye-centred reference frame, but non-visual targets are also stored and updated in an eye-centred reference frame.

3. Neurophysiological and functional imaging evidence

In addition to these behavioural studies, functional magnetic resonance imaging (fMRI) studies in humans and direct recording studies in non-human primates have demonstrated neural correlates of eye-centred spatial remapping. Eye-centred updating of remembered visual space has been shown (both in humans and monkeys) in many brain areas, particularly sub-regions of the posterior parietal cortex (PPC). In monkeys, neurophysiological recordings have shown remapping of reach targets specifically in the medial intraparietal (MIP) area, while predictive remapping of saccadic targets has been shown in the lateral intraparietal (LIP) area, superior colliculus (SC), frontal eye field (FEF), and extrastriate areas. We discuss this evidence in detail below.

fMRI studies using human participants have found that saccade and hand-related areas of PPC were active for memory guided saccades and reaches to peripherally viewed targets in the contralateral visual field (Medendorp, Goltz, Vilis, & Crawford, 2003). That is, a *remembered* target that was seen on the left caused activation in the right PPC. More importantly, when the eyes moved to the right (opposite) side of the remembered target, the activation in PPC shifted to the left (opposite) hemisphere, demonstrating that the target location had in fact been remapped as a function of the remembered target's new location relative to the new gaze direction. This remapping of the remembered object locations has also been shown when subjects merely had to attend to the remembered location in both the PPC (Merriam, Genovese, & Colby, 2003), and extrastriate areas (Merriam, Genovese, & Colby, 2007).

The modulating PPC activity reported in the human neuroimaging studies described above is coincident with activity in the analogous MIP area in the parietal reach region (PRR) of the monkey brain, which shows evidence of eye-centred updating of visual reach targets (Batista, Buneo, Snyder, & Andersen, 1999). Other neurophysiological studies in monkeys have also shown target coding (but not updating) in MIP (Buneo, Jarvis, Batista, & Andersen, 2002; Buneo & Andersen, 2006; Pesaran, Nelson, & Andersen, 2006). However, while Batista et al. (1999) showed updating for reach targets, predictive or anticipatory updating has never been shown for reach targets, but has been for saccadic targets. Specifically, anticipatory remapping of visual space has been shown in neurons in area LIP (e.g., Duhamel, Colby, & Goldberg, 1992; Vaziri, Diedrichsen, & Shadmehr, 2006). It is anticipatory/predictive updating of visual space that allows for the perception of visuospatial constancy spoken about earlier.

Duhamel et al. (1992) propose the following mechanism for anticipatory updating. Efference copy signals of planned eye movements allow neurons to modify firing rates in anticipation of a saccade that will bring a target into, or out of, its receptive field. In

response to a planned eye movement, the neuronal activity shifts accordingly with the impending shift of the retinal image. This creates a dynamic link between retinal images across the eye movement, allowing continuous remapping of visual space in eye-centred coordinates. It is in this way that predictive or anticipatory changes in firing rates contribute to the construction and maintenance of a stable representation of our visual world (Duhamel et al., 1992). The real advantage of this type of forward model is that remapping visual space anticipatorily provides an estimate of the target location prior to the availability of visual and proprioceptive feedback following a shift in gaze. In other words predictive remapping overcomes delays in sensory feedback. A predicted target location can then be compared with the sensory feedback once it is available (Vaziri et al., 2006). Predictive remapping has also been shown to occur in an eye-centred reference frame in neurons in the SC (e.g., Walker, Fitzgibbon, & Goldberg, 1995; Dunn, Hall, & Colby, 2010), the FEF (e.g., Cassanello & Ferrera, 2007; Crapse & Sommer, 2008; Umeno & Goldberg, 1997), and extrastriate areas (e.g., Nakamura & Colby, 2002).

Importantly, there is also an anticipatory response when the location of a previously displayed stimulus is about to be brought into the receptive fields of 44% of neurons recorded in LIP by Duhamel and colleagues (1992). This means even the memory of visual space is predictively remapped relative to the new position of the eyes (as shown in the analogous areas of human PPC by Medendorp and colleagues described above). The predictive remapping of *remembered* space is of critical importance because many of the tasks that we perform on a daily basis rely on visuo-spatial memory. For example, when someone reaches for a cup of coffee while working at a computer, they usually look to the cup and back to the screen before reaching for the coffee. This reaching movement, then, is based on the remembered location of the cup, which has since become peripherally displaced relative to gaze. This intervening eye movement would require predictive remapping of the remembered location of the cup relative to gaze, and in turn the way in which we direct our hand to it.

In addition to efference copy signals, neurons also have access to proprioceptive information of eye orientation, and of course retinal information, both of which also make a contribution to neuronal activity. For instance, neuronal firing rates in area 7a of the inferior parietal lobule (IPL) are modulated by images brought into or out of their receptive fields, by both retinal position and by the position of the eye in the head (Andersen, Essick, & Siegel, 1985). For example a neuron may fire preferentially when an image is projected on the retina 5° to the left of the fovea, and may also fire preferentially when the eye is rotated in the head to the left. If the eye were rotated in the head to the left, and while in this position there was also an image projected on the retina that was 5° to the left of the fovea, then the firing rates of these neurons would modulate multiplicatively. That is, retinal and extraretinal information (i.e., proprioception) is combined resulting in neuronal gain fields for which firing rates for varying retinal displacements are modulated in magnitude as a function of eye position relative to the head (Zipser & Andersen, 1988; Andersen, Snyder, Batista, Buneo, & Cohen, 1998; Snyder, Batista, & Andersen, 1998). While this type of activity modulation is important in the process of using visual information to direct action, it is useful at a later stage of movement generation. That is, it is likely more related to the linkage geometry comparisons required for motor implementation than it is to the updating of visual space *per se*. Visuospatial updating can be more directly related to the compensation for eye movements (resulting in changes in retinal position) by the use of efference copy signals of the eye movements (available before the eye movement is initiated) as described earlier, than by the combination of retinal and proprioceptive information described here. In

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