AGE-RELATED DECLINE IN SENSORY PROCESSING FOR LOCOMOTION AND INTERCEPTION

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Abstract—The ability to control locomotion through the environment and to intercept, or avoid objects is fundamental to the survival of all locomotor species. The extent to which this control relies upon optic flow, visual direction cues or nonvisual sensory inputs has long been debated. Here we look at the use of sensory information in young and middle-aged participants using a locomotor-driven interceptive task. Both groups of participants were asked to produce forward displacements in more or less impoverished environments by manipulating a joystick and to regulate, if necessary, their displacement velocity so as to intercept approaching targets. We show that the displacements produced by the middleaged participants were more nonlinear in comparison with young participants. The errors in the middle-aged group can be accounted for by a constant bearing angle (CBA) model that incorporates a decrease in the sensitivity of sensory detection with advancing age. The implications of this study to a better understanding of the mechanisms underlying the detection of the rate of change in bearing angle are discussed. © 2011 IBRO. Published by Elsevier Ltd. All rights reserved.

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What perceptual-motor organization is involved in the control of goal-directed locomotion? This question has motivated a large number of studies over the last decade, which have led to important insights into the underlying mechanisms (e.g., Rushton et al., 1998; Warren et al., 2001; Wilkie and Wann, 2002; Bastin et al., 2006a; Fajen and Warren, 2007). Taken together, these studies have shown that participants can take advantage of the perceptual information available in the perceptual flow produced by their displacements, so as to produce online locomotor adjustments. This perceptual-motor dialogue can be formalized through task-specific laws of control linking a movement parameter to a perceptual information (Warren, 1988, 2006). The underlying idea of such laws, which express the circularity of the relations between information and movement, is that some invariant properties in the perceptual flow specify the current state of the relationship

*Corresponding author. Tel: +33-491172202; fax: +33-491172252. E-mail address: antoine.morice@univmed.fr (A. H. P. Morice). *Abbreviations:* AE, absolute error; CBA, constant bearing angle; IP, interception point; SSE, sum of squares error.

linking an agent to his/her environment. This dynamically updated relationship would allow functional locomotor adaptations to take place, which in turn would modify the perceptual flow, and so on and so forth.

Following this logic, specific laws of control have been shown to account for the regulation behavior of participants performing heading tasks (Warren et al., 2001; Wilkie and Wann, 2003), locomotor pointing tasks (Warren et al., 1986) or interceptive tasks (Chardenon et al., 2004). Interceptive tasks have deserved a special interest, not only because many daily activities rely on the ability to intercept and/or to avoid moving objects (in sport, in driving, or while walking in a crowded street), but also because they can provide insights about the central control of actions characterized by severe spatial-temporal constraints. It has been suggested that individuals intercepting moving targets rely on a law of control (Eq. 1) which links the subjects' acceleration to the rate of change in bearing angle (Chapman, 1968; Chardenon et al., 2002; Lenoir et al., 2002, see Fig. 1). The bearing angle corresponds to the angle subtended by the current position of the target and the direction of the subjects' motion. This type of strategy for controlling self-displacements during interceptive tasks is known as the constant bearing angle (CBA) strategy.

Using the CBA strategy, the moving object will be intercepted if the observer cancels any change in the bearing angle by accelerating or decelerating accordingly. An increase in bearing angle informs the participant that he/she will reach the interception point before the target and tells him/her to decelerate accordingly. Conversely, a decrease in bearing angle informs the participant that the object will reach the interception point before him/her and prompts him/her to accelerate accordingly. Finally when the bearing angle is kept constant, no change in velocity is required to intercept the target. The participant will intercept the moving object if he/she succeeds in maintaining his/her current velocity. The CBA strategy can be modeled by relating the participant's acceleration to the rate of change of the bearing angle, with a damping term allowing the system to match the required value smoothly and to avoid oscillations around the stable state (Fajen and Warren, 2003; Wann and Wilkie, 2004; Bastin et al., 2006a) (Eq. 1).

$$\ddot{\mathbf{Y}} = k_1 \times \frac{1}{1 + 200 \times e^{(-10 \times t)}} \times \dot{\theta} + k_2 \times \dot{\mathbf{Y}} \qquad \text{(Eq.1)}$$

In this equation, \dot{Y} and \ddot{Y} are the participant's speed and acceleration, respectively, $\dot{\theta}$ is the rate of change of the

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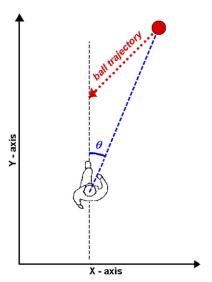


Fig. 1. Bird's eye view of the experimental layout. Participants produced forward displacements on a rectilinear path and aimed to intercept balls that crossed their displacement axis with an angle of 45°. Optical angle of interest is the bearing angle θ . For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.

bearing angle, k_1 is a parameter that modulates the strength of the coupling between the acceleration and the rate of change of the bearing angle, and k_2 is a parameter that modulates the strength of the damping term. The

function $\frac{1}{1+200\times e^{(-10\times t)}}$ is an activation function.

The use of the CBA strategy has been evidenced in studies which have manipulated task constraints such as ball speed (Lenoir et al., 2002), angle of approach (Chardenon et al., 2005) or ball trajectory curvature (Bastin et al., 2006a). In these studies, the CBA model could explain as much as 80% of the total kinematics variance. Interestingly, the CBA strategy can also explain children's (from 10 to 12 years old) locomotor behavior while intercepting moving balls (Chohan et al., 2008) and locomotion produced by different animal species (fishes, dragonflies) while intercepting prey (Lanchester and Mark, 1975; Olberg et al., 2000).

Since the generalization of the CBA strategy appears well established, recent investigations have focused on the sensory signal that the brain uses for detecting the rate of change in bearing angle. The global optic flow field produced by the moving observer has been identified as a power source of information for detecting this rate of change (optic flow signals) (Chardenon et al., 2004). Indeed, because the focus of expansion specifies the direction of the observer's motion, an easy way to detect the bearing angle is to relate the current position of the mobile to the focus of expansion. The detection of the bearing angle remains possible, however, in the absence of optic flow, provided that the observer is able to relate the current position of the object to his/her midline body axis. This egocentric frame of reference is built through the integration of body-related signals, in particular those coming from the vestibular apparatus and from the extra-ocular and neck muscles (Paillard, 1987; Jeannerod, 1991; Blouin et al., 2007). Moreover, the accuracy with which participants refer a moving object with respect to their body can be improved when body-fixed visual references are present in the environment (e.g., a dashboard when driving, a handlebar when cycling; Wilkie and Wann, 2002).

Several studies have been designed to determine how the different sources of information are integrated for detecting the rate of change in bearing angle (Chardenon et al., 2004; Fajen and Warren, 2004). These studies are all based on the same methodology which involves in rendering irrelevant a given source of information (e.g., the focus of expansion no more specifying the actual direction of displacement) and recording the behavioral consequences of this experimental manipulation. Such information manipulation has been achieved, for instance, by laterally displacing the ground plane during self displacement in virtual reality, so as to make irrelevant the position of the focus of expansion (Chardenon et al., 2004), by displacing visual landmarks materializing the midline body axis (Bastin and Montagne, 2005) and by vibrating the neck muscles (Bastin et al., 2006b) in order to bias the egocentric encoding of the target motion direction. Taken together. these studies have shown that the different perceptual signals contribute jointly to the detection of the rate of change in bearing angle. However, the weighting of the signals during this integrative process appears highly context-dependent. The optic flow signal would have the greatest weight when the visual environment is well structured (Bastin and Montagne, 2005; see Warren et al., 2001 for a similar result with heading tasks). In visually impoverished environments, the egocentric frame of reference would gain in importance (Bastin et al., 2006b).

It is worth noting that all the experiments reviewed so far put the emphasis on the perceptual-motor mechanisms allowing young adults to control goal-directed locomotion. In the present experiment, we focused on the much less documented effect of age on these control mechanisms. Aging is generally associated with a decrease in performance in various sensorimotor tasks, including interceptive tasks (Spirduso and MacRae, 1990). This performance decline is known to appear even in moderately advanced age (e.g., 50-60 years, Sarlegna, 2006). Factors contributing to the elders' deficit in intercepting moving objects could include increased perception thresholds in the detection of motion (Warren et al., 1989; Tran et al., 1998; Andersen and Enriquez, 2006) especially for translational motion (Billino et al., 2008). Here we tested whether providing visual information that is known for being informative of the speed and direction of the participant's displacement (e.g., optic flow, body-fixed visual landmark) can help middle-aged adults to compensate, at least partly, for the deteriorating effect of aging during an interception task. We also tested young adults for comparison. The second (related) aim of the experiment was to test to what extent the bearing angle strategy (Eq. 1) could account for the locomotor adjustments produced by the two groups of participants.

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