

## Review article

## Understanding the roles of vision in the control of human locomotion

Aftab E. Patla\*

*Neural Control Lab, Department of Kinesiology, University of Waterloo, Waterloo, Ont. N2L 3G1, Canada*

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**Abstract**

This review focuses on advances in our understanding of the roles played by vision in the control of human locomotion. Vision is unique in its ability to provide information about near and far environment almost instantaneously; this information is used to regulate locomotion on a local level (step by step basis) and a global level (route planning). Basic anatomy and neurophysiology of the sensory apparatus, the neural substrate involved in processing this visual input, descending pathways involved in effecting control and mechanisms for controlling gaze are discussed. Characteristics of visual perception subserving control of locomotion include the following: (a) intermittent visual sampling is adequate for safe travel over various terrains; (b) information about body posture and movement from the visual system is given higher priority over information from the other two sensory modalities; (c) exteroceptive information about the environment is used primarily in a feedforward sampled control mode rather than on-line control mode; (d) knowledge acquired through past experience influences the interpretation of the exteroceptive information; (e) exproprioceptive information about limb position and movement is used on-line to fine tune the swing limb trajectory; (f) exproprioceptive information about self-motion acquired through optic flow is used on-line in a sampled controlled mode. Characteristics of locomotor adaptive strategies are: (a) most adaptive strategies can be implemented successfully in one step cycle provided the attention is biased towards the visual cues: only steering has to be planned in the previous step; (b) stability requirements constrain the selection of specific avoidance strategies; (c) response is not localized to a joint or limb: it is global, complex and task specific; (d) response characteristics are dependent upon available response time; (e) effector system dynamics are exploited by the control system to simplify and effectively control swing limb trajectory. Effects of various visual deficits on adaptive control are briefly discussed. Copyright © 1997 Elsevier Science B.V.

**Keywords:** Vision; Human locomotion; Visual deficits; Adaptive control

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**1. Introduction**

Locomotion is an integral part of many life-sustaining and -enhancing behaviours such as searching for food, and going on a favourite hike. The ability to go over or under obstacles and use isolated footholds of various surface characteristics allows legged animals to traverse terrains that are virtually inaccessible to wheeled vehicles [1,2]. Rich sources of sensory input in general and visual input in particular, make it possible

to adapt the rudimentary gait patterns for travel over varied, cluttered and uneven terrain.

The visual system is uniquely positioned to provide information on the static and dynamic features of the near and far environment in which an animal lives and moves. Sense of smell can provide limited information about living things; auditory information can also be useful in locating other animals (with limited precision) provided of course they are not silent. Vision, on the other hand, does not have these limitations and is the only sensory system that can provide information about inanimate features at a distance. Estimates of rates of information (contained in light's intensity, direction,

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\* Tel: + 1-519-8884567, ext. 3535; Fax: + 1-519-7466776; E-mail: patla@healthy.uwaterloo.ca.

frequency and polarization) transmitted in the visual system range from  $10^6$  to  $10^8$  bits/s [3]. The Bible's first imperative 'Let there be light' is understandable for this queen of the senses [4]. Visuomotor transformations involved in locomotion have provided the evolutionary building material for the fine prehensile control of upper limbs [5]; therefore, understanding the roles of vision in control of locomotion has far-ranging implications.

This review focuses on how visual input is acquired, processed and transformed into motor output during locomotion in a varied, cluttered and uneven environment. Various roles played by the visual input in guiding the locomotor act, the properties of visual perception and the characteristics of locomotor adaptive strategies are discussed. A brief introduction on the effects of various deficits and its effect on locomotion follows. The review ends with the challenges and opportunities facing researchers in this exciting area.

## 2. Identifying the roles of vision in control of locomotion

A necessary first step to understanding the roles played by the visual system in regulation of locomotion, is to outline the requirements that the locomotor control system has to satisfy [1]. The locomotor machinery should be able to (as listed by Patla [1]):

- (a) Set up the initial body posture needed to initiate locomotion.
- (b) Initiate and terminate locomotion as and when needed.
- (c) Produce and co-ordinate the rhythmic activation patterns for the muscles of the limbs and the trunk to propel the body in the intended direction.
- (d) Maintain dynamic stability of the moving body counteracting the force of gravity and other forces (expected and unexpected)
- (e) Modulate the patterns to maintain or alter the speed of locomotion, to avoid obstacles, select appropriate stable foot placement, accommodate different terrains and change the direction of locomotion.
- (f) Guide locomotion towards endpoints that are not visible from the start.
- (g) Use minimal fuel to maximise distance covered before stopping for replenishment of nutrients.
- (h) Ensure the structural stability of the locomotor apparatus to minimise downtime or permanent damage during the lifespan of the animal.

These requirements are not desirable but necessary features, although on a short-term basis the system may be able to function, for example, if the last two requirements are not rigidly satisfied. Vision plays a critical role in the control of dynamic stability, in adapting the basic patterns for various environments and in guid-

ance of locomotion towards endpoints not visible from the start (as outlined above in (b), (d), (e) and (f)). The first three are local objectives that have to be satisfied on a step by step basis while the third objective is global and is involved in route planning. Consider these in some detail.

### *2.1. Visual input is essential for implementing avoidance strategies critical for proactive regulation of dynamic stability during locomotion*

Sensory modalities such as the kinesthetic and vestibular systems, by detecting unexpected perturbations, play an important role in reactive control of balance. Reactive control should be the backup and not the front line of defense. Imagine the potential damage to tissues not to speak of the state of your mind should a trip followed by successful recovery be the only way we could accommodate obstacles in the travel path. The most powerful means of ensuring stability is to proactively avoid the perturbation altogether. Identification and avoidance of potential threats to stability are made possible by the visual system. Vision, as discussed before, can provide us with information from a distance almost instantaneously because of the high speed of propagation of light waves. This allows us to interpret and take appropriate anticipatory action before reaching the site of potential perturbation. These actions are classified as avoidance strategies [6], and include the following: (a) selection of alternate foot placement by modulating step length and width, (b) increased ground clearance to avoid hitting an obstacle on ground and increased head clearance to avoid hitting an obstacle above ground, (c) changing the direction of locomotion (steering) when the obstacles cannot be stepped over or under, and (d) stopping. Clearly, avoidance strategies represent proactive locomotor adaptations that are primarily implemented to ensure dynamic equilibrium of the moving body.

### *2.2. Visual input is essential for proactive adjustments necessary for accommodating different surfaces in the travel path*

During travel we often encounter surfaces with different geometrical properties such as sloped surfaces or staircases, and surfaces with different material properties such as a soggy field or ice. This will influence the body-ground interaction [6]. Unlike avoidance strategies which normally would influence one or two steps, accommodation strategies would usually involve modifications sustained over several steps. The types of changes made to the normal locomotor rhythm may include those discussed under avoidance strategies. For example, while walking on an icy surface step length is often reduced. Other changes include a change in locus

of propulsive power as found in stair climbing (propulsive power from the muscles around the hip and knee joint) [7] compared to level walking (major propulsive power from muscles around the ankle joint) [8].

The initial planning of gait adjustments during a transition from a normal level surface to a different surface has to be visually mediated. We have shown how subjects alter their foot placement (and body posture) and velocity based on the visually perceived surface compliance characteristics [9]. Once the foot contact has been made with the altered surface, other sensory modalities, in particular the kinesthetic system, can come into play in the modulation of gait patterns. While there is a considerable body of work documenting the characteristics of avoidance strategies, work on accommodation strategies is limited.

### *2.3. Visual input plays an important role in route planning for navigation to destinations that are not visible from the start*

Locomotion is goal directed. When the route or path and the end goal is visible from a single viewpoint, visual input alone can guide locomotion. In general, the end goal is not visible from the start. We navigate using stimuli that have no predictable relationship to the final destination [3]. Among the many navigational strategies available to move in a large-scale spatial area, humans predominantly use the strategy of piloting [10–12]. Piloting strategy requires mental representation of the spatial areas [3]; cognitive spatial maps stored in the various neural substrates are these mental representation. Poucet [13] has discussed the nature of these spatial maps, which contain allocentric information (spatial information independent from ones location). These maps contain combination of topological and metric information. Topological information about relative relationships between landmarks in the environment, is useful when obstacles constrain the use of a particular travel path. The ability of animals to take shortcuts implicates metric representation of space. The cognitive maps we store are not like the cartographic maps that we can buy. Spatial representation is non-homogeneous: places that have more value to us (for example a church or a cinema) are stored while other landmarks in the vicinity (say a fabric shop) are omitted. The ability to store and retrieve spatial information about large environments gives us independence and confers mobility that is not slavishly tied to sensory stimuli within the field of perception.

Another navigational strategy called 'dead reckoning' used by humans to return to the start position without the use of any landmark cues: return path is computed from the distance and the direction traveled from the start [3]. The range and precision over which this non-visual guidance of the locomotion operates is limited

[14]. Researchers have argued that distance and direction traveled can be obtained from integration of vestibular signals; kinesthetic system can also provide estimates of linear distance traveled. Since the integration process is easily corrupted by noise in the sensory system, the strategy can only operate over short distances unless the deviations from the desired path are corrected by 'visual fixes' of environmental landmarks [15].

Therefore, it is clear that recognition of landmarks provided by vision and control of steering in which vision plays a crucial role, are integral to the navigation process.

## **3. Basic anatomy and neurophysiology of the visuomotor transformation**

### *3.1. Sensory apparatus is designed to detect spatio-temporal pattern of light over range of intensities and distance*

Eyes used for extracting information from light are often erroneously compared to a camera. Both have convex lenses that focus the image on a surface that is sensitive to light energy: but there the similarities end. Whereas in a camera images at different distances are brought into focus by changing the distance between the lens and the film, in the human eye the focal length of the lens is altered to ensure that the image falls on the retinal surface. The film in a camera contains light-sensitive material distributed uniformly on the film surface and can capture static images. The light-sensitive receptors on the retina in a human eye are distributed unevenly and are able to capture dynamic images [3]. Different types of receptors (rods and cones) have different sensitivity to light; some receptors are sensitive to different wavelengths allowing detection of colour [3]. The human retinal surface is divided into two main regions: the fovea located in the center (10° of visual field) which has a high density of cones giving high visual acuity in bright light and the peripheral region surrounding the fovea which contains primarily the receptors that are more sensitive to light (rods) giving low acuity vision in dim light [3]. Through light and dark adaptation (this process takes time) we can see over different ranges of light intensity, as witnessed by our ability to detect many features in a darkened room after we are in it for a while. The concentration of the light-sensitive receptors in the two eyes located on the face provide some visual field overlap and depth perception. The visual field is approximately 200° in the horizontal plane and 110° in the vertical plane. The ability to move the eyes within the head and the head with respect to the body allows us to scan the environment beyond the specific visual field of view without

having to reorient the whole body. The spatio-temporal pattern of light which contains information about the environment is detected by the receptors in the retina and converted into a spatio-temporal pattern of activity in the optic nerves. How the information contained in the spatio-temporal pattern of the light is extracted by the central nervous system is discussed next.

### *3.2. Afferent inputs from the retina are processed in parallel by different visual cortical areas to extract different attributes such as colour, motion and form*

Visual input from the retina are primarily processed in the cortex [16]. Primary visual cortex receives retinal input via the lateral geniculate nucleus and parcels this to various surrounding cortical areas responsible for processing the visual input. Neurophysiological and clinical studies show that these visual areas are devoted to extracting specific visual attributes from the visual scene such as motion and form [16]. Since these attributes have clear adaptive value and the processing required to extract these are different, functional specialization of visual cortical areas has taken place [16]. The two major streams of visual processing from the primary visual cortex are the occipitoparietal (to posterior parietal cortex) and occipitotemporal (to inferotemporal cortex). These were proposed as 'where' and 'what' pathways [17], but have recently been revised by Milner and Goodale [18] to serve two major functions of vision, perception and action. Perceptual constancy requires us to visually recognise objects and events in different contexts and from different viewpoints, while control of action demands visual input from an egocentric perspective. It is not surprising therefore that visual processing for these two roles served by vision is different and dominated by different cortical streams. Retinal inputs are also processed subcortically by the superior colliculus which has been shown to play an important role in orienting and attention to novel stimuli in the visual field [19]. The parallel and modular processing of visual input from the retina confers speed and flexibility and allows us to control whole body movements such as locomotion.

### *3.3. Frontal and parietal cortex and the hippocampus have been implicated in cognitive spatial mapping*

Identification of neural sites for cognitive spatial maps have relied on animal and human lesion studies and animal electrophysiological studies. Animal studies have shown that various cells in the hippocampus are tuned to code location of the animal (called place cells) and the direction that the animal is travelling in (called direction cells [11,13]. Lesions of the hippocampus in animals lead to a variety of spatial problems, though similar lesions in humans affect declarative memory

and not procedural memory which would play a role in guiding locomotion [20].

Lesions in the parietal cortex affect acquisition and retention of spatial information, although egocentric (body referenced) spatial information is unaffected. Damage to the frontal cortex on the other hand, affects egocentric spatial information while allocentric information is unaffected. Current thinking as reviewed by Poucet [13] attributes the following roles to various neural substrates in humans. Hippocampus is proposed as a site for coding topological information, while the parietal cortex which receives visual and somatosensory input provides metric representation of the allocentric space. The frontal cortex along with the striatum transforms this allocentric spatial information into appropriate spatially directed locomotor movements in the egocentric frame [21].

### *3.4. Corticospinal tract is actively involved in visually mediated locomotor adaptive strategies while the Tectospinal tract is involved in orienting to stimuli in the visual field*

Visual input can through intermediate structures such as the cerebellum influence the activity in many descending tracts which in turn modulate the locomotor activity. But primarily researchers have identified two major descending tracts, the corticospinal tract originating in the motor cortex and tectospinal tract from the superior colliculus, which play a dominant role in visuo-locomotor control. Superior colliculus which receives retinal input is as discussed plays an important role in orienting behaviour (primarily head and trunk movement but may also involve whole body reorientation) to visual stimuli; control is exerted through the tectospinal tract.

The activity in the corticospinal tract has been studied in considerable detail while the animal is walking on a treadmill [22]. When there are no obstacles present, and no specific foot placement is required the corticospinal activity is minimal. In contrast, when the animal is required to visually regulate the swing limb trajectory for obstacle avoidance or specific foot placement, the corticospinal tract becomes very active [22]. Neuronal activity codes limb elevation (separate bursts for the lead and trail limb) and foot placement [22], and can depending on the intensity reset the locomotor rhythm. How the visual information processed in the occipitoparietal stream (subserving action) is transformed into corticospinal tract output is not clear [23].

### *3.5. Control and stability of gaze during locomotion is achieved by various reflexive and volitional mechanisms*

During locomotion, the eyes can be subjected to changing acceleration within a step cycle. While hori-

Table 1  
Various reflexive and volitional mechanisms available to stabilize gaze

Type	Mechanism	Role
Reflex	Vestibulo-ocular reflex (VOR)	Compensate for head rotation in the three planes by using canal inputs
	Cervico-ocular reflex (COR)	Neck receptors take over the role of VOR if the vestibular system is affected
	Opto-kinetic response (OKR)	Compensate for non-visual mechanisms (VOR and COR) by detecting retinal image slip
Volitional	Saccadic eye movements	Shift of spatial attention by rapidly moving the eyes (to minimize visual disturbance) towards eccentric targets of interest
	Smooth pursuit movements	Track selected object of interest by potentiating visual feedback from the relevant area of the retina (requires cortical involvement)
	Vergence eye movements	Eyes moving in opposite direction to fixate on targets that are at different distances from the observer to ensure binocular alignment (also involves concurrent changes in focal length of the lenses)

zontal acceleration of the head is attenuated to about 25% of the horizontal acceleration experienced by the hip joint through anticipatory control of paraspinal muscles [24], vertical acceleration of the head is virtually similar to the vertical hip acceleration. This constant jarring, if uncorrected, can lead to blurring of the visual image on the retina, which is clearly undesirable. Researchers have shown clearly that the head (and by inference gaze) is stabilized while the subjects are walking: pitch rotation and vertical displacement of the head co-vary to provide stability of the head in the sagittal plane during locomotion [25]. Similar control of head position has been demonstrated in the frontal plane [26]. Various reflexive and volitional mechanisms available to track and stabilize gaze on targets of interest are summarized in Table 1 [27]. These mechanisms are necessary to allow the fovea (central visual field) to extract appropriate details of objects in the environment, and also for the peripheral visual field to extract self-motion information from the optic flow.

#### 4. Characteristics of visual perception

##### 4.1. Intermittent visual sampling is adequate for safe travel over various terrains

Visual system resources can be shared for the execution of other tasks, while sensory information from the kinesthetic and vestibular system is usually dedicated when the body is moving. We are able to, for example, admire the scenery while walking. Researchers have used various experimental paradigms to show that intermittent sampling of the environment is adequate [28–30]. This finding is not surprising considering evolutionary pressures which required the predator or the prey to attend to other things while locomoting. Our work [30] has shown that when the terrain is even and no specific foot placement is required, subjects visually sample the environment for less than 10% of the travel

time (not including the initiation and termination phase); when foot placement is constrained (by requiring the subjects to step on specific locations) the sampling time increases to slightly over 30% with subjects sampling every stride for longer duration ( $\sim 500$  ms) or every step for shorter duration ( $\sim 250$  ms) (Fig. 1).

##### 4.2. Information about body posture and movement from the visual system is given higher priority over information from the other two sensory modalities

Kinesthetic and visual inputs, unlike vestibular inputs, can be misinterpreted by the nervous system. When the support surface moves (for example while standing on a compliant surface) the kinesthetic output can be in error because its output is referenced to the support surface. Similarly, since the visual system detects relative motion between the body and the environment, environment motion can be perceived as self-motion. The three sensory modalities with their different frames of reference [31] should help to resolve conflict when one of the sensory system outputs is in error. The information from the visual system, however, can override veridical information from other sensory modalities as demonstrated by the elegant studies of Lee and his colleagues (see review by Lee and Young [32]). For example rotation of the room in which a person is running, leads to compensatory rotation of the trunk to orient the body with respect to the visual surround [32]. Work by Lackner and DiZio [33] in a rotating room and by Pailhous et al. [34] using projected visual flow, produce powerful perceptual illusions demonstrating the dominance of visual input over other sensory input.

##### 4.3. Exteroceptive information about the environment is used primarily in a feedforward sampled control mode rather than on-line control mode

Theoretically, any sensory based regulation of move-

ment is a form of feedback control. However, as discussed before, vision provides information about events and environments at a distance almost instantaneously. This makes it possible to use the information in a predictive fashion to plan proactive adjustments of locomotor patterns. We have used various experimental paradigms to show that exteroceptive information about an obstacle for example is used in a feedforward manner to regulate swing limb trajectory [30,35,36]. The fact that continuous vision is not necessary for guiding locomotion has already been discussed.

Consider voluntary visual sampling data while subjects approach and step over obstacles in some detail to bring home the point that exteroceptive information is used in a feedforward sampled control mode [35]. As seen in Fig. 2, voluntary visual sampling in the approach phase (from start to before the lead limb steps

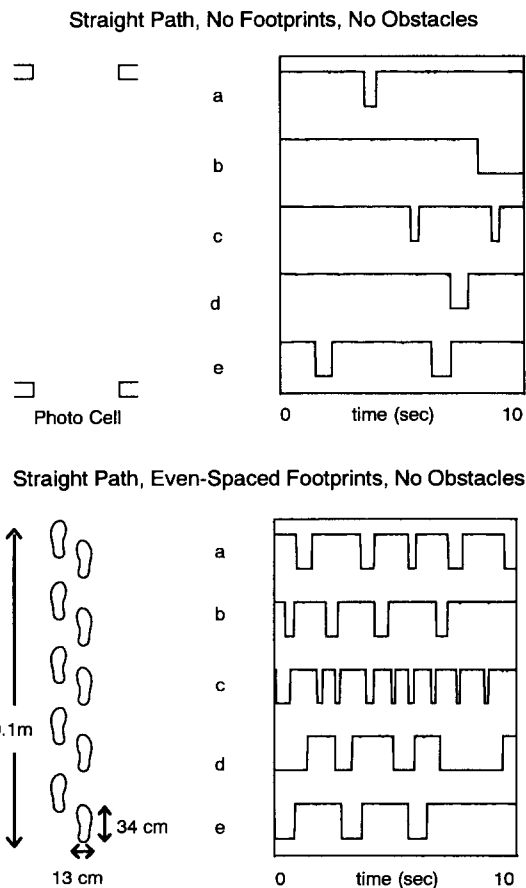


Fig. 1. Voluntary visual sampling patterns are shown for five subjects while they were required to walk along a straight path with no foot placement requirement and on a straight path with evenly spaced footprints. Subjects wore liquid crystal glasses that are normally opaque (give non-specific ambient light with no form or motion information): the glasses can be made transparent when subject presses on a hand held switch resulting in a passage of current. Top line of each graph represents the opaque state for the glasses and when the signal is below this baseline the glasses are transparent. Sampling demands increase as expected when subjects are required to step on the footprints.

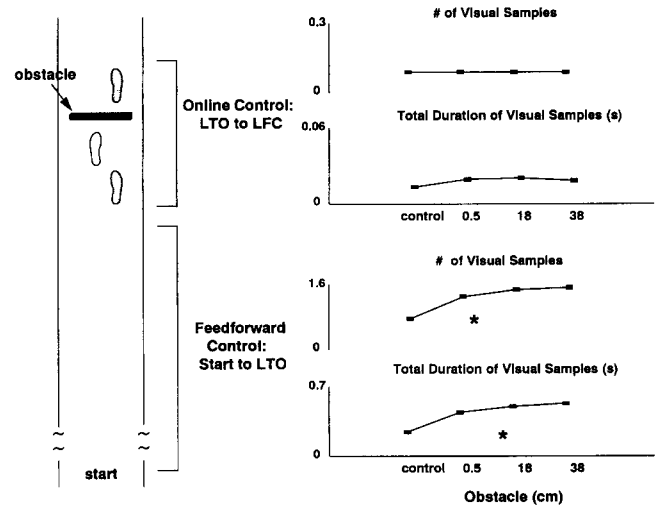


Fig. 2. Voluntary visual sampling characterized (no. of visual samples and total duration of visual samples) as subjects approach (feedforward control phase: from start to lead limb toe-off (LTO)) and step over obstacles of different heights (on-line control phase: lead limb toe-off to lead limb foot contact after the obstacle). An asterisk indicates that the measures were significantly modulated as a function of obstacle height. These results show that exteroceptive information is used in a feedforward mode rather than in an on-line control mode (adapted from Patla et al. [30]).

over the obstacle) is modulated as a function of obstacle height. In contrast, voluntary visual sampling as the lead limb steps over the obstacle is minimal and is unaffected by the presence or absence of obstacle of any height. Recently, we have measured gaze behaviour during an obstacle avoidance task and showed that subjects do not fixate on the obstacle in the step before or as they step over the obstacle [36]. Others have monitored eye movements during visually guided stepping [37] to show the feedforward nature of visual control.

These findings are not surprising since environmental features such as obstacles which require gait adaptations are generally static and do not alter their shape or size: therefore, on-line monitoring of footholds (for specific foot placement) or obstacles (for stepping over or under) is not necessary. In instances where, for example, an obstacle does change size (when a pet suddenly decides to stand up or an obstacle topples over), peripheral visual input can and is used on-line to modulate swing limb trajectory (Quevedo and Patla, unpublished data).

The nature of exteroceptive information that we use to build our perceptual experiences is different from the information necessary for guiding movement, as discussed before. To step over an obstacle such as a toy we need to know its height, width and location; its shape or colour is not relevant (unless it provides additional information about other characteristics) [38]. To recog-

nize the toy on the other hand, shape and colour are important.

#### 4.4. Knowledge acquired through past experience influences the interpretation of the exteroceptive information

Several researchers argue that all the information necessary for guidance of action such as locomotion is available in the spatio-temporal pattern of light falling on the retina (see Gibson [31]): no inferences or indirect perception is needed to extract meaningful information. While this proposition has merit, it is also clear that knowledge acquired through past experience plays an integral role in interpreting visual information. As Gregory [39] has pointed out, an image of a glass is not brittle; our past experience tells us so, which helps us when we approach and grasp such an object. Similarly, a person who steps on an icy surface for the first time will have considerable difficulty making the appropriate proactive adjustments based on visual input (about the surface) alone.

Therefore, both visually observable and visually inferred properties of the environment influence the avoidance strategy selection and implementation [6]. We have shown, for example, that perceived fragility of the obstacle influences the amount of toe clearance [40] (Fig. 3). Another example of cognitive influence is when an obstacle avoidance response has to be initiated quickly; subjects show a two-stage modulation of limb trajectory; initial large change is in response to obstacle followed by finer adjustments related to the height of the obstacle [41].

#### 4.5. Exproprioceptive information about limb position and movement is used on-line to fine tune the swing limb trajectory

Once again using obstacle avoidance paradigm as a probe, we have shown that visual input about limb

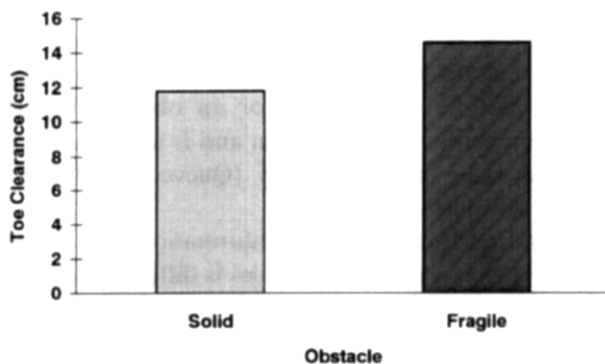


Fig. 3. Average toe clearance over a solid and a fragile obstacle of same height, demonstrating that visually inferred properties influence locomotor adaptive strategies (adapted from Patla et al. [40]).

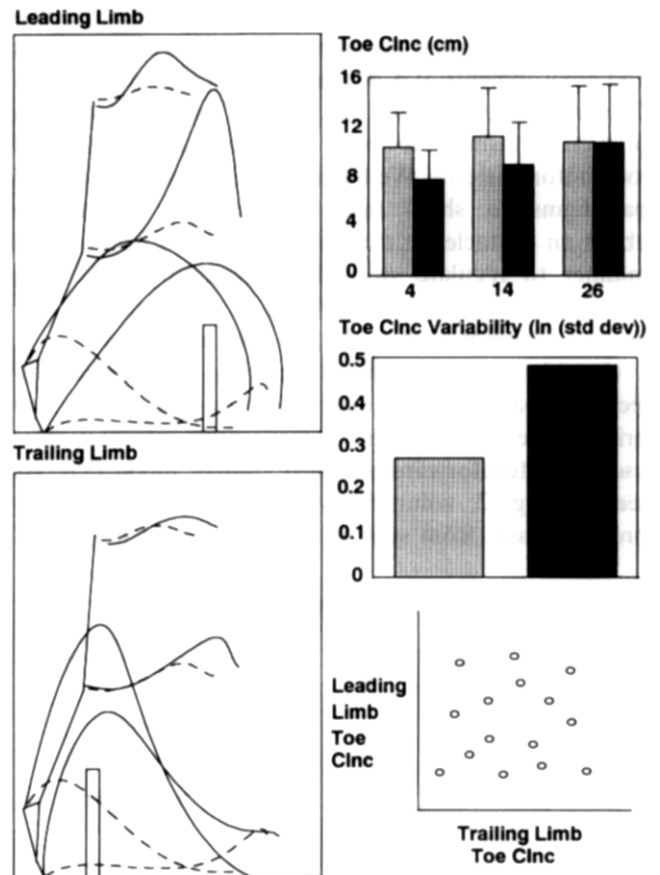


Fig. 4. Average and variability of toe clearance over obstacles of different sizes are shown along with typical spatial ( $y$  versus  $x$ ) trajectories of the lead and trail limb as they step over an obstacle in the same stride. Lead limb measures, lightly shaded bars; trail limb measures, darkly shaded bars. The bottom right hand panel shows that lead and trail limb toe clearance within the same stride are not correlated suggesting that the trajectories are controlled relatively independently (adapted from Patla et al. [40]).

position and movement (called exproprioceptive by Gibson [31] to distinguish it from proprioceptive input provided by the kinesthetic system) is used to fine tune the swing limb trajectory [35,40,42]. For example the toe clearance variability of the lead limb (where the visual input about the limb is available) is lower than the toe clearance variability of the trail limb (where the visual input about the limb is unavailable [40] (Fig. 4).

#### 4.6. Exproprioceptive information about self-motion acquired through optic flow is used on-line in a sampled controlled mode

Vision provides the only direct measure of self-motion (or egomotion) which is useful for regulating velocity of locomotion and steering (see review by Warren [43]). Vestibular input, besides being unable to detect constant velocity, needs to be processed along with relevant kinesthetic input (from the neck to distinguish whole body motion from head motion) to provide a

measure of self-motion. It is not surprising therefore that, during normal locomotion, vestibular influence on the skeletal muscles is reduced [44] to ensure that head movements used to visually scan the environment do not inappropriately affect locomotor patterns. Similarly, kinesthetic input from the distributed receptors can only give an indirect estimate of whole body velocity.

Many studies have shown that optic flow during locomotion has a powerful influence on whole body velocity in humans [33,34,43,45]. These optomotor responses (vision directly driving locomotion) show clearly that optic flow (detected primarily by the large peripheral field of view) is used by the nervous system to regulate velocity of locomotion. Recently, we have expanded on this research and have shown that continuous vision is not necessary for the accurate detection of optic flow: a 200 ms sample every stride is sufficient to prevent the drift (because of poor speed regulation) observed when vision is denied during treadmill walking [46] (Fig. 5). Thus, visual input about self-motion is used on-line in a sampled control mode to control the speed of walking.

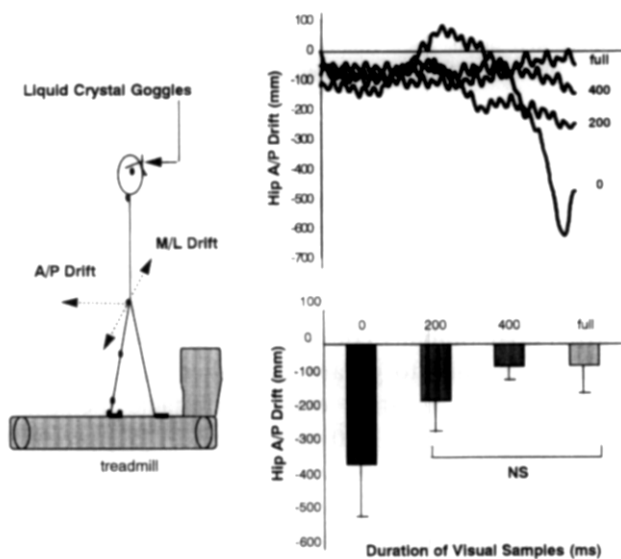


Fig. 5. A schematic diagram of the experiment shows that the subjects were required to walk on a motorized treadmill while wearing liquid crystal glasses described in Fig. 1. Hip position in the anterior-posterior (AP) directions as a function of time are shown when subjects had full vision, no vision (0), or a 200 ms or 400 ms visual sample every stride. Visual sampling was manipulated in the middle of a 10 s trial, with the first 5 s showing the hip position under normal vision condition. The bottom right hand graph shows the maximum drift (posterior displacement) under various visual sampling conditions; the drift values under 200 ms or 400 ms were not statistically significant from the full vision condition. This demonstrates that relevant exproprioceptive information about self-motion can be acquired in a sampled rather than continuous mode (from Dubrowski and Patla [46]).

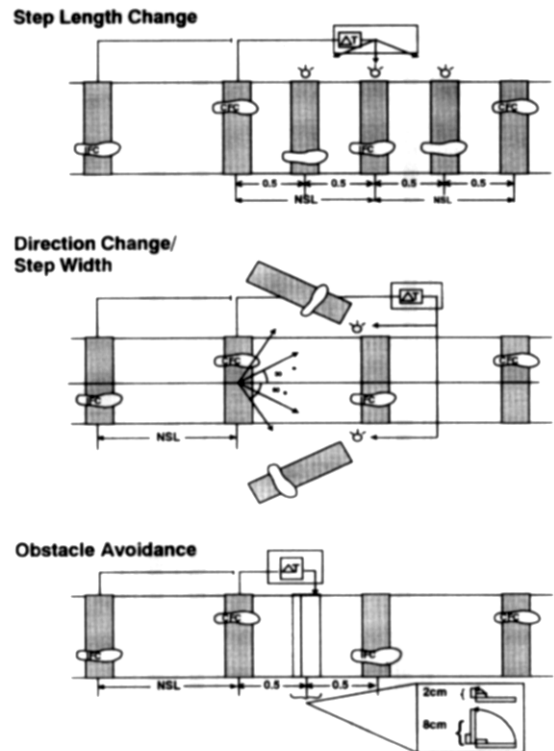


Fig. 6. Bird's eye view of the travel paths used in various experiments where subjects were required to alter step length or width (specified by light cues beside the appropriately placed mats) or step over obstacles (plates that were elevated to a vertical position from a horizontal position) under different time constraints ( $\Delta T$ ).

## 5. Characteristics of locomotor adaptive strategies

*5.1. Most adaptive strategies can be implemented successfully in one step cycle provided the attention is biased towards the visual cues: only steering has to be planned in the previous step*

We have used a variety of experimental paradigms (seen in Fig. 6) manipulating the times available for implementing adaptive strategies based on visual input. These studies have shown that the minimum time (expressed in terms of the step cycle metric) required for implementing most avoidance strategies is one step cycle [47–49]; success rates required for implementing strategies for adjusting step length, step width, stepping over or under obstacles is greater than 80% when a visual cue is available one step ahead (Fig. 7). In contrast, steering has to be planned in the previous step cycle: success rate is near zero when only one step cycle duration is available for changing direction (Fig. 7).

In these experiments the subject's attention is biased towards the visual cues. During natural locomotion, our attention could be directed elsewhere. Since we have a finite visual field of view (as discussed before), attention to something else can adversely affect the minimum time needed for successful implementation of



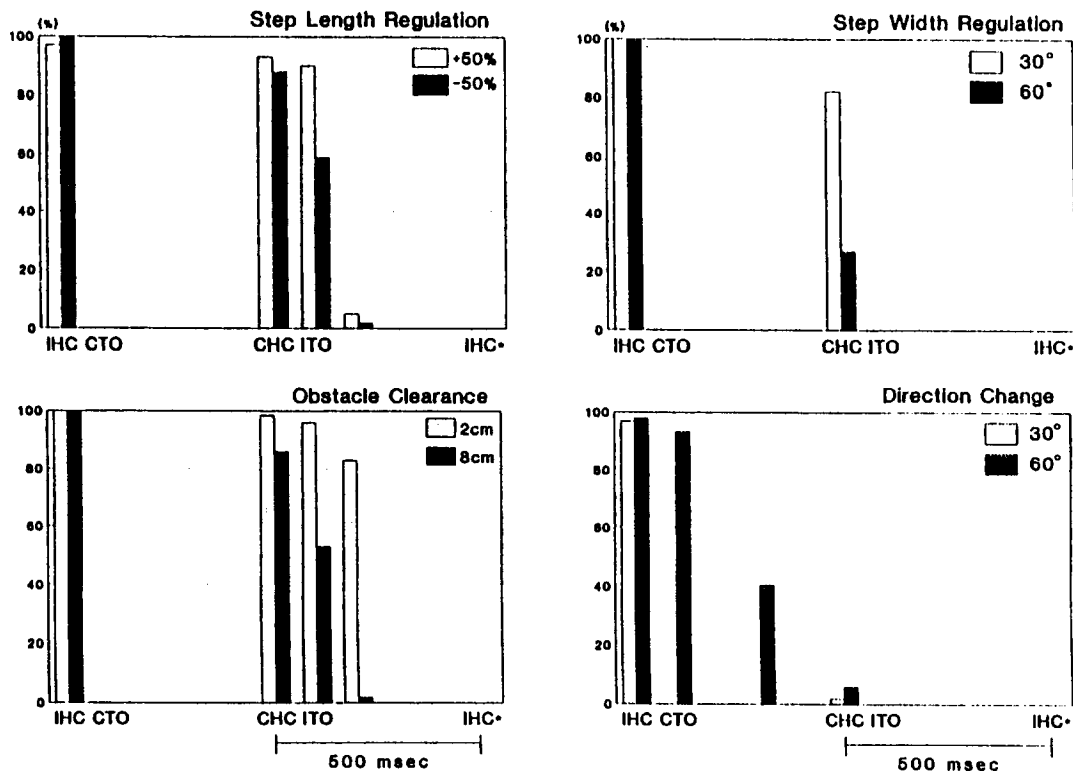


Fig. 7. Summary of success rates for various avoidance strategies when cues were given at different times during the step cycle. Experimental paradigms used are shown in Fig. 6. Note that the asterisk, besides ipsilateral heel contact, represents the event following successful implementation of avoidance strategies. The 500 ms value represents average step duration. The success rates are plotted as a function of when the visual cue to alter step length, step width, direction change or obstacle clearance were given. These results show that most adaptive strategies can be successfully implemented in one step cycle: only steering control has to be planned in the previous step cycle (from Patla [6]).

avoidance strategies. In a recent experiment we asked subjects to either avoid an obstacle above ground (situated at head height level) or one on the ground (height 20 cm): the probability of occurrence of the two obstacles were manipulated such that obstacle at head level was presented four times more often than the obstacle on the ground. Success rate for the low obstacle in this experiment was very low (Fig. 8), even though, when the low obstacle was presented by itself, subjects had no difficulty in successfully stepping over (Fig. 8). Zohar [50] in an observational study showed similar results.

### 5.2. Stability requirements constrain the selection of specific avoidance strategies

In the experimental paradigms shown in Fig. 6, visual cues not only specified when to initiate a change but also instructed the subjects to implement a specific avoidance strategy. While these experiments served a useful purpose, they clearly do not simulate naturally occurring visual cues which have to be processed and a decision to select a specific avoidance strategy has to be made. The decision to go around versus step over an obstacle appears to be guided by the dimension of obstacle size scaled to body size. As seen in Fig. 9,

when the obstacle height is about equal to the lower leg length (i.e. the ratio is a near one) most subjects, given a choice, prefer to go around rather than step over. This change in action mode triggered by a dimensionless parameter relating environmental features to body size has been explained in terms of affordances (see Warren [51]). Stability consideration may be the driving factor in deciding to go around rather than step over. Although limb elevation over an obstacle includes a large safety margin ( $\sim 10$  cm clearance) [52] precision of control is not great: variability (across trials) increases as a function of obstacle height [40]. Therefore, the risk of tripping increases as we step over obstacles of greater height and it is understandable that given a choice we decide to go around larger obstacles.

To decode the rules guiding selection of alternate foot placement, we have used an experimental paradigm where the instruction to the subject was to avoid stepping on a light spot projected on the travel path. By manipulating the location, size and shape of the light spot we were able to tease out the rules for the selection of specific foot placement through step length and width regulation (Fig. 10) [49].

The results (Fig. 10) show that selection of alternate foot placement is not random but guided by simple

rules. Minimum foot displacement from its normal landing spot is a critical determinant of alternate foot placement position. When two or more choices meet the above criteria, modifications in the plane of progression are preferred. Given a choice between shortening or lengthening step length, subjects chose increased step length; inside foot placement is preferred over stepping to the outside provided the foot does not cross the midline of the body. Recently Chen et al. [53] have also shown that subjects prefer to lengthen their step rather than shorten their step length. As discussed by Patla et al. [49], these rules for alternate foot placement selection ensure that avoidance strategies are implemented with minimal changes to ongoing locomotor activity while maintaining the dynamic equilibrium and allowing the person to travel forwards safely.

### 5.3. Response is not localised to a joint or limb: it is global, complex and task specific

Locomotor pattern changes for step length and width regulation, stepping over and under obstacles and steering have been characterized at the kinematic, kinetic

and muscle level [47,48,52,54–57]. The picture that emerges from these experiments shows that response is not localised to a joint or even a limb but is rather global and task specific. Modulations of ground reaction impulses have been used to arrive at laws of perception-action coupling [57]. Fig. 11 captures the signature impulse patterns for various locomotor adaptive strategies during the braking and push-off phases of the stance limb, and highlights the complexity of control. Consider the characteristics of muscle activity patterns that produce these ground reaction forces (and hence impulses).

The changes in muscle activity patterns are not simple amplitude scaling of the normal locomotor patterns: rather both ipsi and contralateral limb muscle activation patterns show phase (of the step cycle) and muscle specific modulations as seen for stride length increase in Fig. 12. The form of locomotion (walking versus running) also influences the strategies adopted to achieve, for example, stride length regulation (Fig. 12). Both stance and swing limb muscles contribute to what is primarily changes in the swing limb trajectory [47,48,52,54,56,58] (Fig. 12). Although most avoidance strategies are limited to a single step, when environment demands gait adaptations over multiple steps, strategies for successive steps influences the strategies used for the current step [59].

### 5.4. Response characteristics are dependent upon available response time

A common observation made by researchers studying reactive balance control strategies is that the responses are very much dependent on when (and hence where) in the step cycle a perturbation is applied [60,61]. Visually guided proactive strategies show similar time-dependent response characteristics [47,48,52,54,62]. Consider avoidance of obstacles above ground [62]. As expected, to achieve head clearance subjects controlled the head and trunk movements. When there was enough time to execute the response trunk motion was primarily restricted in the pitch plane: in contrast when time was limited, roll motion of the trunk was recruited to assist the forward pitch motion in achieving appropriate head clearance [62] (Fig. 13).

### 5.5. Effector system dynamics are exploited by the control system to simplify and effectively control swing limb trajectory

Knowledge about the plant is important for the design of any control system. The control system that takes advantage of any unique properties is considered a better design from an engineering perspective. It is, therefore, not surprising that nature has learnt to ex-

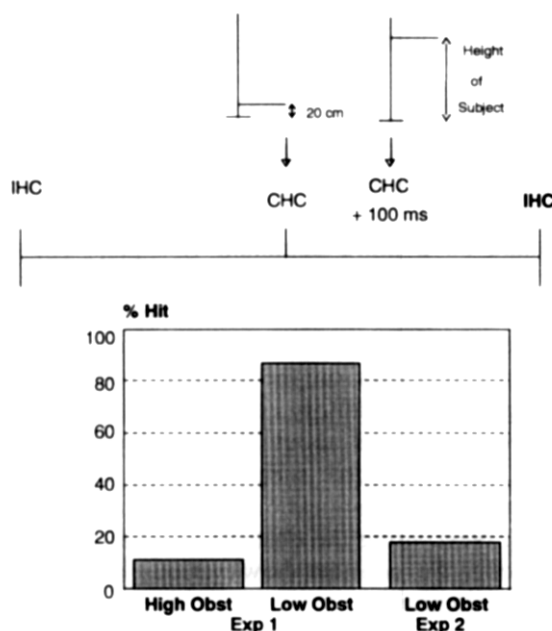


Fig. 8. Schematic diagram of the experimental setup shows when the signal to trigger the low obstacle (20 cm high) or high obstacle (at head level) were given. The success rates for stepping over the low obstacle or stepping under the high obstacle for two experiments are summarized below. In the first experiment probability of a high obstacle appearing was 40%, low obstacle 10% and no obstacle (control trials) 50%. In the second experiment the probability of a low obstacle appearing was 50% and no obstacle (control trials) 50%. These results demonstrate how the minimum time for successful implementation of avoidance strategy can be influenced by biasing the subject's attention (from Patla, unpublished results).

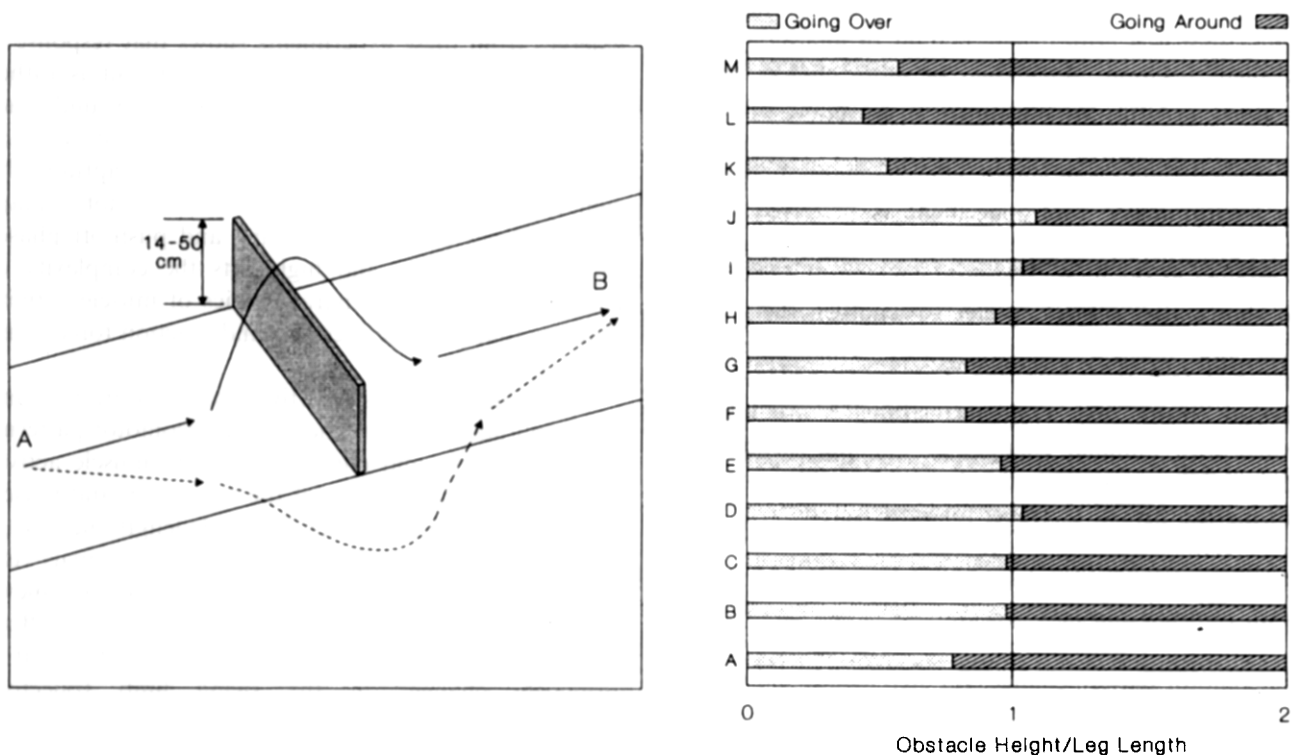


Fig. 9. Schematic diagram of experimental setup shows that subjects were required to go from A to B; when an obstacle (of different heights) was present in the travel path they had a choice to step over or go around it. Results from the experiment are plotted as a function of obstacle height/leg length. When this ratio is one, most subjects chose to go around rather than step over the obstacle. Note the subjects K, L and M were the shortest subjects in the experiment. These results show that selection of action mode (stepping over or going around) is based not on absolute obstacle height but rather obstacle height scaled to each subject's size (as reflected in the lower leg length) (from Patla, unpublished observation).

exploit the features of the effector system to simplify control of movement and achieve economy at the same time (see review by Smith and Zernicke [63]). Empirical and modelling work have clearly shown that passive dynamics of the swing limb play a dominant role in the expression of the swing limb trajectory: active muscle control is used to fine tune the trajectory [64]. Recently, we have shown that intersegmental dynamics are utilised during adaptive locomotion to achieve limb elevation over obstacle [55]. Hip and ankle joint flexion of the swing limb are achieved not by active muscle work, but by motion dependent torques generated by active control at the knee joint [56] and stance limb action at the hip joint. Modelling work has shown that the strategy of using stance limb muscles to hike the hip joint and achieve swing limb elevation is the most efficient [65].

## 6. Effects of visual system damage on adaptive locomotion

During normal unperturbed straight path locomotion, the role of vision is, as would be expected, minimal. When vision is compromised, adaptive

locomotion suffers. Even with a complete loss of vision limited purposeful locomotion is still possible. In blind individuals, auditory, haptic and olfactory systems take on a more dominant role [66]. The cane used by these individuals extends their haptic exploration to at least one stride length ahead (determined by the length of the cane) [67] to give them advanced warning of obstacles on the ground or a change in surface geometry. Auditory cues provided by cane tapping give useful cues about surface properties. Sense of smell, from a source such as bakery can serve as useful landmark identification for purposeful navigation [66]. Next, using the obstacle avoidance paradigm as a probe, we consider how various deficits affect adaptive locomotion.

### 6.1. Adverse effects due to damage to sensory apparatus can be partially compensated

Consider three common eye diseases: age-related cataracts, age-related maculopathy (ARM), and loss of one eye. As we age, development of cataracts, a common age-related eye disease, has a tremendous impact on mobility. Effects of cataract on obstacle avoidance show increased toe clearance and greater variability in

limb elevation, particularly over low obstacles [68] (Fig. 14). Loss of foveal vision is a common visual pathology affecting over 25% of the elderly population. We have studied how age-related maculopathy influences locomotion over different travel paths and stepping over obstacles [69–71]. A key finding from the performance on an obstacle avoidance task by these patients was increased toe clearance over small low contrast obstacles [71], suggesting that loss of contrast sensitivity and acuity affects the ability of subjects to accurately judge the height of these obstacles (Fig. 14). Epidemiological studies show increased difficulty with low-lying low contrast obstacles [72] in individuals with visual deficits; findings from studies on cataract patients and patients with ARM help us understand these epidemiological data.

Monocular vision has been shown to adversely affect the control of upper limb movements [73]; loss of visual field and an important source of depth perception influences pre-planning and on-line control of movement. Recently we studied healthy subjects stepping over obstacles under monocular and binocular viewing

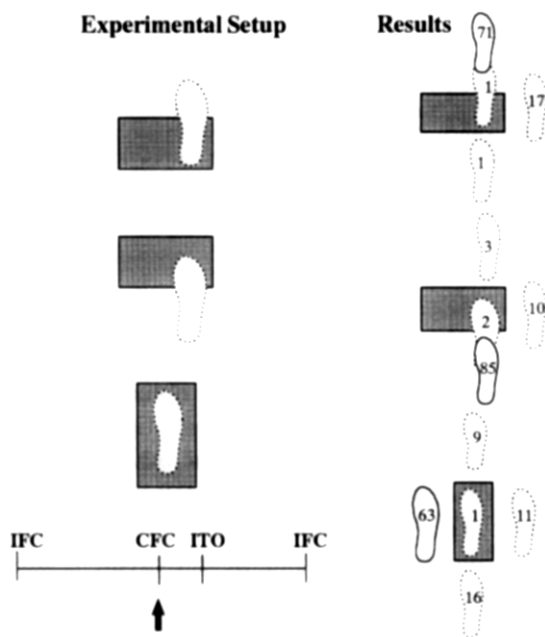


Fig. 10. Schematic diagram of the experimental setup shows light spot on the travel path (shaded bar) which the subjects were instructed to avoid; if they were unsuccessful approximate position of the foot is shown. The signal for the appearance of the light spot was one step before (contralateral foot contact). The alternate foot placement chosen by the subjects are shown by the location of the foot with the numbers representing percentage of times subjects chose the particular foot placement. The dominant strategy is shown by the footprint in the solid line. These results suggest that the selection of alternate foot placement is not random, but guided by rules which are discussed in the text (from Patla et al. [49]).

Type of Strategy	Goal: Bias the Ipsilateral Limb Trajectory	Braking	Push-off
Normal			
Obstacle Clearance			
Short Step			
Long Step			
Step Wide			
Direction Change			
Stopping			

Fig. 11. A schematic diagram detailing the changes (indicated by the length of the appropriate line) to the three orthogonal linear impulse components ( $I_x$ ,  $I_y$ ,  $I_z$ ) and one angular impulse component ( $H_y$ ) in the two stance phases (Braking and Push-off) during the implementation of various avoidance strategies. These signature patterns highlight the complexity in the control of locomotor adaptive strategies (from Patla [6]).

condition [42]. Monocular viewing introduces greater variability in perceptual estimate of obstacle height, influences the choice of limb to lead over the obstacle and toe clearance over the obstacle [42] (Fig. 14).

These results show deterioration in adaptive control as seen in higher variability of toe clearance which has the potential to increase the risk of tripping. Increased average toe clearance represents compensatory adaptation to deficits in the sensory apparatus.

## 6.2. Damage to ventral stream (occipito-temporal) of visual processing spares the use of vision in guidance of movement such as locomotion

So far we have primarily looked at deficits in the peripheral visual sensory apparatus. How damage to various visual cortical areas affects adaptive locomotion has been relatively unexplored: when patients with selective damage are studied the focus has been primarily on visual perception [74]. Recently we studied a patient who suffered visual form agnosia from carbon

monoxide poisoning on the obstacle avoidance task. While her perceptual abilities such as verbal estimation of obstacle height are severely compromised; her ability to use vision to guide locomotion over uneven terrain is remarkably well preserved [75] (Fig. 14). This mirrors the earlier findings on the preservation of visually guided upper limb movements in the same patient [76].

## 7. Concluding remarks

Advances in our understanding of the various roles

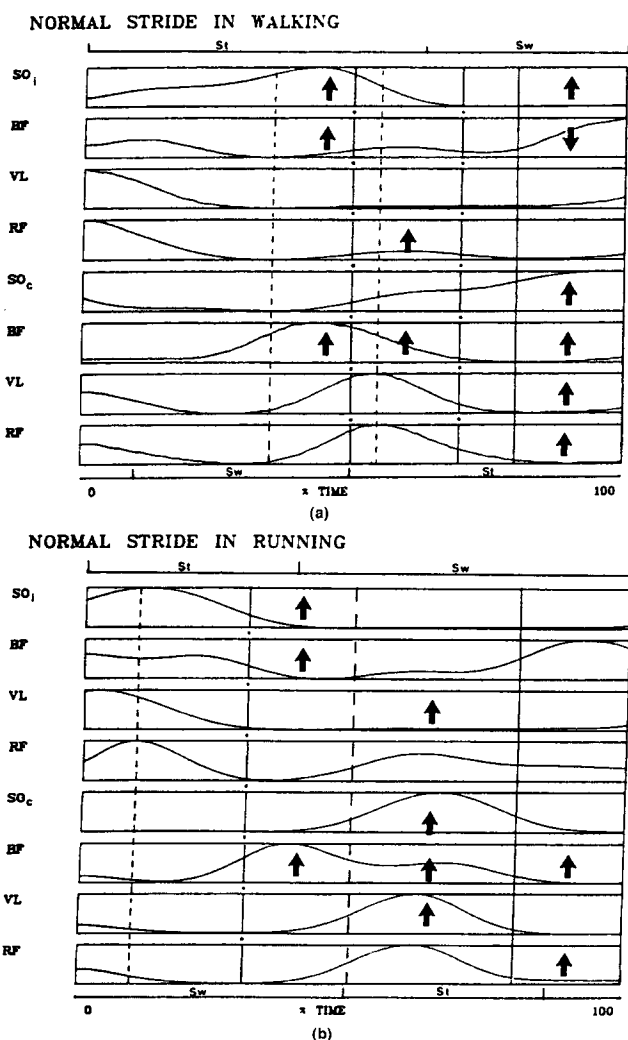


Fig. 12. A summary of increase or decrease in muscle activity for specific phases are superimposed on normal activity profiles for walking (a) and running (b). The changes were observed when subjects were required to increase their stride length in response to an audio cue given at the beginning of the stride (0%). The results show complex changes in both stance and swing limb muscles required for locomotor adaptive strategy and also the influence of the form of locomotion on the response (from Patla et al [54]).

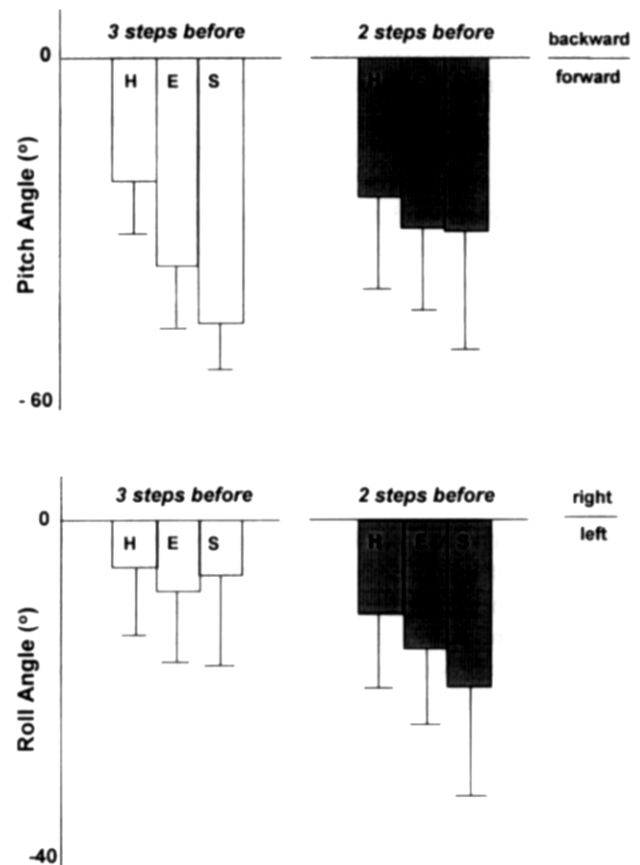


Fig. 13. The pitch and roll angular displacement of the trunk when the subject was under an above ground obstacle are shown for two conditions (when subject had either three or two steps to plan a response). The results clearly show that response characteristic is influenced by the time available for implementation (adapted from Patla [62]).

played by vision in the control of human locomotion have been reviewed. Like the Roman God Janus with one face looking to the past and the other towards the future, in this review I have also hopefully attempted to highlight what we do not know about visual control of human locomotion. Decoding neural circuitry subserving visuo-locomotor control, characterizing accommodation strategies for various surfaces, and expanding our understanding of visual sampling characteristics are some of the challenges facing researchers in this exciting area.

## Acknowledgements

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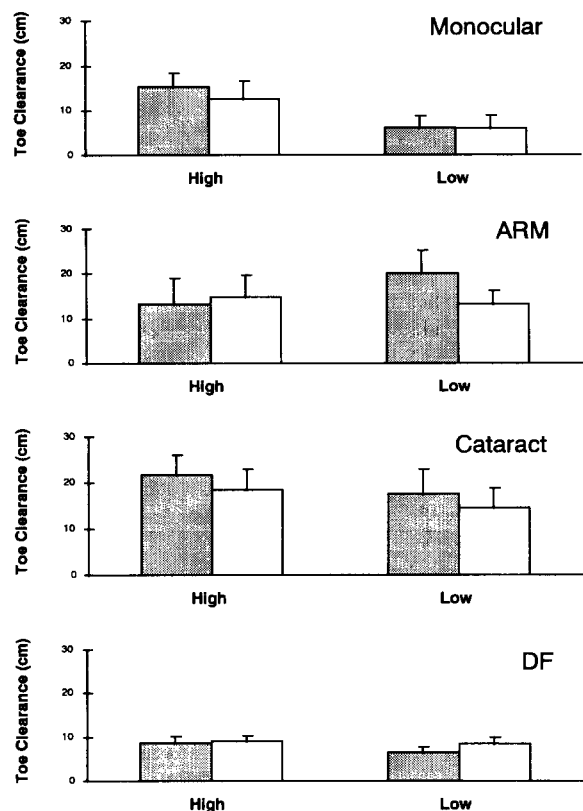


Fig. 14. Toe clearance values over low and high obstacles for subjects with various deficits (shown in lightly shaded bars) are compared with appropriate controls (shown in darkly shaded bars). Subjects under monocular viewing condition were compared to the binocular viewing condition. Age matched healthy subjects were used as controls for comparison with patients with age-related maculopathy (ARM), age-related cataract and a patient (DF) with damage to the ventral stream of visual input processing. (Adapted as follows: Monocular, from Patla et al. [42]; ARM, from Patla et al. [71]; Cataract, Adkin et al. [68]; DF, Patla and Goodale [75].) Note that the size of the high obstacles was the same (27 cm); the low obstacle was 10 cm high for DF compared to 7 cm for all others.

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