Visually guided locomotion and computation of time-to-collision in the Mongolian gerbil (Meriones unguiculatus): Probing the neural substrates.

by

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A thesis
presented to the University of Waterloo
in fulfillment of the
thesis requirement for the degree of
Doctor of Philosophy
in
Psychology

Waterloo, Ontario, Canada, 2000

0-612-53515-0

Borrower's Page

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Abstract

In a set of four experiments this study set out to replicate and extend the findings of Sun, Carey, & Goodale (1992) of the use of time-to-collision (t-t-c) in a visually guided task in Mongolian gerbils, and then investigated the effects of lesions to different cortical areas. In the first three experiments gerbils were trained to run in the dark toward a target on a computer screen. On some trials, the target changed in size as the animal ran toward it in such a way as to produce "virtual targets" that appeared closer than or farther away from the real target, if the animals were using t-t-c information. In Experiment 1, it was confirmed that gerbils use time-to-contact information to modulate their speed of running toward a target, but the results show that it is not the only source of information used. Experiment 2 established a cortical role in the use of time -to-collision as it was established that visual cortex lesions attenuate the ability of lesioned animals to use information from the visual target to guide their run. Control frontal cortex lesioned animals were able to use t-t-c information to modulate their deceleration, but their runs were different from those of shams. Experiment 3, showed that small radio frequency lesions, of either the primary visual cortex, or the lateral extrastriate regions of the visual cortex also affected the use of t-t-c. It is possible that the animals in Experiment 1 and the sham animals in Experiment 2 detected the target as moving in some trials, and the differences between sham and frontal lesioned animals seen in Experiment 2 may have reflected deficits in processing this object motion by the frontal lesioned animals. This hypothesis was tested with a changed protocol in Experiment 4, and while some trends in the predicted direction were seen, the results were not convincing enough to confirm the role that frontal and lateral extrastriate areas play in the processing of object motion, as compared to the processing of t-t-c information.

Acknowledgements

I would like to thank my supervisor, Dr Colin Ellard for directing my attention to this area of research, and guiding me with patience throughout this project. Grateful thanks to my thesis committee members, Dr Pat Wainwright, Dr Barb Bulman-Fleming, Dr Heather Carnahan, and Dr Douglas Wong-Wiley for their critical evaluation and insightful comments. Thanks to Dr Hong-Jin Sun, Dr Linda Cudmore, Dr Marla Bigel, and Dr Mike Dixon for their helpful advice on various issues.

Many thanks to Nancy Gibson for her expert and diligent animal care. Kathy Blom's patient lessons in histology are much appreciated. Thanks to Gerry Blom and Bob Ewert for revamping the runway, and Bill Eickmeier for doing some of the software programming.

Grateful thanks to Dave Machachek for giving me my first lessons in using the Scion imaging tool and Sharon Scovil for training animals for the last study. My son Rohan's knowledge of features and shortcuts in various computer programs helped me immensely in data depiction and in compiling my thesis. Sarah Shaughnessy and Rick Byers cheerfully provided help during stressful times at the end of my research period.

I would like to thank my friends, Louise Scott, Jelena Pavlovic, Heather McNeely, Todd Girard, Dave Westwood, Renee Dolomount, and Christina Gojmerac for providing cheer and encouragement through all these years.

I would like to acknowledge my family in India: my parents, Col and Mrs. EN Pillai, for their unconditional love and support, and for providing a stimulating intellectual environment; my in-laws, Dr and Mrs. VS Nair, for their encouragement and pride; and my three older brothers for all their terrific achievements: I had no choice but to try and keep up.

Lastly and very importantly, a big thank you to my husband Sanjeev for all his support and for doing more than his share of parenting over the past few years, so I could complete this work. I thank my precious boys, Rohan and Sameer for their love, and patience with a forever-busy mom.

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INTRODUCTION

Vision plays an important role as organisms move about in the environment by giving them the information they need to regulate their behaviour. James Gibson coined the phrase "optic flow" in the 1950s to refer to the continuously changing optic array that arises from textural surfaces in the environment as an observer travels through it. He proposed that the varying patterns of light rays that reach the eye as an animal moves provides information about the layout of the environment. Gibson (1950) set the stage for a direct theory of perception, describing the dynamic visual input from optic flow, rather than a succession of static images, as being central to the act of perception. Since the 1970s progress in the field of studying optic flow and it's related optic variables has been rapid, encompassing both animal and human studies. The range of experimental studies has included simple psychophysical paradigms, to robotics, to virtual-reality experiments, as well investigations into the neural basis of the use of optic flow in different species of animals.

The purpose of this dissertation is to describe experiments dealing with an optic variable called time-to-collision (t-t-c)(Lee, 1976), and to report on the findings of lesion studies that were undertaken to probe the neural underpinnings of the use of t-t-c in gerbils. The focus of the first experiment was to replicate and extend the work of Sun, Carey, and Goodale (1992) and determine whether gerbils use t-t-c when running toward a target. Having established that animals use t-t-c to modulate their locomotion during visually guided runs, the next two experiments were conducted to probe the neural underpinnings of this variable through the lesion technique. Experiment 4 was conducted to study the neural substrates involved in processing self-motion cues obtained from t-t-c, and those involved in processing object-motion.

1. Locomotion in the environment

Locomotion through the environment cannot be random or automatic, and controlled only by the brain. The control of movement depends on the animal-environment system (Gibson, 1979), the animal having the capability to monitor the environment and modulate its movement accordingly to successfully negotiate it.

Lee (1977) classified the information that is necessary to control locomotor activity in the environment into three types: a) *exteroceptive*, that is, information about the layout of surfaces and objects in the environment gained largely through vision, b) *proprioceptive*, which includes information about the movement of body parts relative to one another, gained largely through mechanical receptors in the joints, the vestibular system, and through vision c) *exproprioceptive*, that is, information about the position of the body relative to the environment, again gained largely through vision. Thus, locomotion in the environment depends on information gained from the environment that, along with information that an animal receives from its senses, acts together to help it decide its movement.

2. Ecological approach to visual perception

Conventional approaches to the subject of visual perception state that a large number of factors such as distance estimation, velocity of movement, binocular disparity, eye movement need to be factored in on a continuous basis to be integrated and used to obtain a percept of the world. An alternative view, the ecological approach, first developed by Gibson

(1950, 1966, 1979), states that the environment contains readily available spatial and temporal information in the optic array. Optic flow can give three types of information: spatiotemporal, temporal, and three-dimensional spatial information. Spatiotemporal information gives the animal important cues regarding its movement; temporal information allows it to time its action in the environment; and spatial information gives it the layout of the environment. Gibson (1966, 1979) pointed out that animals actively pick up optic flow information from the continuously changing optic array, and use it to modulate their behavioural responses in the environment. In this approach the emphasis is not on a succession of retinal images, but on the explicit information in the changing optic array that informs the animal about the environment as well as its own movement. Optic flow, according to Gibson, provides accurate visual input to navigate in the environment, through monitoring self-motion, avoiding obstacles, and guiding future action. In this view, perception and action are closely interrelated, and each guides the other.

In Gibson's framework, in order to understand visually guided locomotion one has to look at what information is available in the immediate environment to specify spatial and temporal patterns, and how that information can affect an animal's actions. When an animal is moving rapidly in its environment, optical cues such as distance estimation, velocity of movement, etc may not be the best source of rapidly useable information. What is needed then is readily available information that can quickly guide the actions of the animal.

3.Time-to-collision

Most animal species need to continually monitor information about approaching objects, to avoid predators or imminent collision with another object or surface. The rate at which the information has to be processed must be very rapid and is challenging to the visual system.

Developing some of Gibson's ideas, Lee (1976, 1980) proposed that a parameter of optic flow, which he called "tau", could yield information to an observer regarding his movement relative to an approaching surface. Lee (1976) showed that the ratio of retinal image size at a given instant and the rate of expansion of the image could give an accurate measure of the time-to-collision (t-t-c). The inverse of the rate of expansion of the image on the retina is equal to the t-t-c with that object (See Appendix A for the derivation of tau). Lee proposed that the information about the rate of expansion of the retinal image could be extracted by the visual system, without inferring the distance of the approaching object. The t-t-c can also be specified by the ratio of the solid angle subtended at the eye by an object moving toward an observer to the rate of change of this angle (Lee &Young, 1985). According to Lee (1976, 1980), and Lee and Lishman (1977), the visual variable that provides information about t-t-c (τ), and the variable tau (dot), which provides information about the increase of τ, both provide instant predictive information for an animal to control its deceleration to an object or target. The value of tau is independent of the absolute speed of the observer or surface, as well as the size of the object. If an animal or person is able to regulate braking then the rate of change of tau can be kept constant and precisely timed stopping can be possible. Tau does not give information regarding the distance of the surface or target, but provides information on when collision with the object or surface will occur if the movement continues.

Although velocity of a movement will rarely be constant, the value of τ can be used to trigger modulation of visually guided activity. In a situation in which an animal needs to time an action this variable will give it efficient information. If the animal were to gauge its distance from the target, it would be required to monitor its velocity and location, and that could cause unnecessary delays.

Tresilian (1991) classified two different forms of tau, one the "local" tau that specifies local features of the optic flow field, and the other "global" tau that specifies the centre of expansion of a flow field. These different forms of tau will be useful in different situations, for instance, moving toward a prey, or navigating in the environment, respectively.

4. Evidence for the use of time-to-collision

Psychophysical experiments have provided a large body of evidence to show that humans use optic flow to determine their direction of heading, and that the visual system uses this information with other sensory information to infer self-motion. A number of studies in human and non-human species have indicated the more specific use of t-t-c in a variety of tasks (for instance, Lee, 1976; Lee, Lishman, & Thomson, 1982; Lee & Reddish, 1981; Wagner, 1982; Warren, Young, & Lee, 1986).

a. *Human studies*

Defensive responses to objects on a collision course may be based on detection of τ. Studies with human babies and infant monkeys have shown that the perception of optic flow and avoiding objects on a collision course may be innate and not dependent on experience. Bower, Broughton, and Moore (1970) found that babies as young as eight days old, responded with aggrieved reactions when a foam rubber cube was pushed towards them. When the shadow of objects projected on a screen expanded to indicate looming, human babies (Ball & Tronick, 1971) and infant monkeys (Schiff, Caviness, & Gibson, 1962) showed distress reactions.

Schiff and Detwiler (1979) showed that people were able to estimate quite accurately when an approaching object would hit them, irrespective of the background information. With experience in a familiar environment, adults may not show defensive reactions to looming optic flow information, when they believe there is no real danger, as shown by King, Dykeman, Redgrave, and Dean (1992). Savelsbergh and his colleagues (Savelsbergh, Whiting, & Bootsma, 1991; Savelsbergh, Whiting, Pijpers, & van Santvoord, 1993) used a catching task with three luminous balls to show the use of relative optical expansion information. For one of the balls, the time-to-contact information could be manipulated by deflating the ball as it approached the participants on a pendulum, to mimic the slower approach of the other two fixed-size balls. They found that the participants delayed their grasp response for the deflating balls. They found that relative optical expansion information available between 300 and 200 ms before ball-to-hand contact was used in the act of catching the balls.

Konczak (1994) studied the speed of walking in adults moving through a swinging tunnel that altered optic flow effects. He found that walking speed increased in the condition in which the walls of the tunnel moved in the direction of walking, whereas there was no effect on speed of walking when the walls moved in the opposite direction. However, it must be kept in mind that during walking many other cues will be available and the variations in optic flow may not alter walking behaviour as predicted.

Lee and his colleagues (Lee et al., 1982; Warren, et al., 1986) studied activities like long jumping and walking to see if participants used t-t-c information to modulate their actions. They proposed that long jumpers use information from time to contact with the running board to adjust their final few strides before executing a long jump, and that when required to step on irregularly spaced targets, flight length was also monitored by time to contact information.

Lee (1976) has suggested that a driver could use tau to gauge time to contact with a preceding car or obstacle, and the change of rate of tau (tau dot) can then be applied to control braking. In a recent experiment, Sun and Frost (1998a) studied the visual control of braking by human subjects on stationary bicycles. They found that compared to when a target was a stationary, subjects braked sooner in front of an expanding target and conversely they braked later in front of a contracting target. This study indicates that subjects are using information from t-t-c to control locomotion in a braking task.

b. *Animal studies*

Researchers have used behaviour such as landing on surfaces (Borst & Bahde, 1988, Wagner, 1982), and chasing (Wagner, 1986), to study the use of optic flow in insects. Wagner (1982) analyzed films of flies landing on small spheres and compared the coefficient of variation across different variables, such as relative retinal expansion velocity (inverse of changing visual angle), target distance, or visual angle, and found that the ratio of the rate of expansion of the image of the sphere to its size was the least variable measure, showing that flies obtain t-t-c with a landing surface directly from optic flow, and not by distance estimation. He found that the housefly's deceleration before a landing response is triggered when the relative retinal expansion velocity reaches a critical value. This mechanism provides a constant t-t-c for different flight velocities. Lee and Reddish (1981) observed that a diving gannet appears to use t-t-c information to initiate wing streamlining before making contact with the surface of the water. When trying to catch fish, gannets start their dive from a height with their wings in a swept-back posture to allow accurate steering. However, just before they hit the water, the wings have to be streamlined to avoid injury. The timing of the change in wing posture is crucial as it decides steering accuracy as well as avoidance of injury. Lee and Reddish (1981) indicate that the birds are probably using information from when τ reaches a critical value, to streamline their wings at the right time thus maintaining diving speed, as well as avoiding injury. Even though the velocity of a dive increases because of the force of gravity, causing underestimation of tau, the bird uses the information from tau value to modulate its action at an optimal time during its dive.

Davies and Green (1990) compared the variability in different optical parameters (distance, angular change, and t-t-c) used by pigeons and a hawk during extension of feet before landing. They concluded that the hawk used t-t-c information, as this timing was less variable than the distance between the eye and the perch at the point when the feet were extended. They contend that their data do not support the notion that pigeons use tau, because there was less variability in the pigeon's use of distance cues as compared to the use of t-t-c information. It is possible that the two species of birds use different optical cues to guide foot extension when they land, because pigeons are known to use head bobbing when they land, and this would lead to fluctuations in the value of tau, making it an unreliable source.

Sun, Carey, and Goodale (1992), using gerbils, manipulated the size of a target during an animal's approach to it, and then studied its effect on the animal's run, providing a convincing case for the use of tau. They showed that gerbils trained to run toward a target on a computer monitor used information from the changing retinal image of the target to modulate their locomotion.

The diving and landing behaviour studies (Davies & Green, 1990; Lee & Reddish, 1981) have been criticized by Wann (1996) for having biased sampling. For instance, as he points out, conclusions from the Davies and Green (1990) study were based on only four landings from a single hawk. Similarly, the Lee and Reddish (1981) study, though using a bird that dives from great heights, uses data of very short durations, and does not take into consideration factors like air resistance. Some of the experiments mentioned above (Davies & Green, 1990; Wagner, 1982) have depended on an indirect method of evaluating the use of tau, for instance, comparing various strategies that could be used during timing of an action during approach to a surface and then deciding which of those strategies has least variability. Sun et al.'s (1992) study on the other hand manipulated the t-t-c information to study the predicted effects on the gerbil's run, and is a direct method to study the use of t-t-c.

c. *Physiological studies*

The term 'optic flow' is often used to refer to complex patterns of visual motion that can be used to derive subject heading and velocity, but similarities between processing this kind of visual information and the simpler t-t-c variables in the present experiment merit a review of the neural processing of optic flow information.

Insects:

There are many studies that have looked at the neural basis of optic flow detection in insects. For instance, visual interneurons that respond to particular features in the optic flow to aid dragonflies catch prey have been found by Frye and Oldberg (1995), O'Carroll (1993), and Oldberg (1981). Others have identified interneurons that respond to self-motion induced optic flow components in the hawk moth (Farina, Varjù & Zhou, 1994; Kern, 1998; Kern & Varjú, 1998) and flies (Laughlin, 1998). Using a new method, Krapp, Hengstenberg, and Hengstenberg (1998) found ten "vertical system" neurons that responded to particular aspects of self-motion induced optic flow in the third visual neuropil (lobula plate) of the blowfly *Calliphora erythrocephala.* These VS neurons in the fly supply visual information for the control of head orientation, body posture, and flight steering, giving information about self-motion in the fly.

Birds:

Important evidence for the presence of optic flow and t-t-c processing neurons in pigeons has come from electrophysiological studies conducted at two Canadian laboratories over the past few years. Wylie and Frost (1990, 1991, 1999a, b) found neurons in the nucleus of the basal optic root (nBOR) and vestibulocerebellum of the pigeon brain that aid the distinction between rotational and translational optic flow patterns and give the birds important information to aid locomotion. In a more recent article Wylie, Bischof and Frost (1998) show that the translational optic flow neurons are organized as three axes reference frames: the vertical axis, and two horizontal axes oriented at 45 degrees to either side of the body, which is a similar reference frame to the semicircular canals of the vestibular system.

Using single-cell recordings, Wang and Frost (1992) found that a group of cells in the midbrain in pigeons was strongly stimulated by the image of a solid-patterned ball moving in depth, when it was heading in a collision-bound direction toward the pigeon's eyes. This activation was not affected by the size of the stimulus, nor the speed with which it moved.

Mammals:

Rabbits: Cells have been found in various areas of the visual system that are responsive to motion detection and optic flow in other animals. Electrophysiological studies have shown that there are areas in the temporal cortex of rabbit that have cells that are motion sensitive (Chow, Douville, Mascetti & Grobstein, 1977; Mather, Douville & Chow, 1977).

Cats: In the cat, area 18 has been reported (Cynader & Regan, 1978) to have cells that respond well to stimulus motion in depth, and that presumably signal impending collision with an object. Gibson, Baker, Mower, and Glickstein (1978) reported that some cells in area 18 of the cat visual area are directionally selective and respond preferentially to large moving spots. Baker, Gibson, Glickstein, and Stein (1976) found cells with similar properties in the visual pontine area that receive connections from area 18, which they propose might play a role in the visual guidance of locomotion. Another area in the cat visual cortex that subserves the use of motion and optic flow is reported to be the lateral suprasylvian (LS) cortical area. Zeki (1974) had proposed that the LS area in cats and the MT area in primates might be analogous because of similar response properties of the cells. Rauschecker, von Grunau, and Poulin (1987) found cells in LS that were responsive to motion along radial lines originating at the centre of gaze similar to optic flow. Other researchers too have found evidence that supports the notion that the LS area is responsive to optic flow stimuli (Kim, Mulligan & Sherk, 1997; Mulligan, Kim, & Sherk, 1997; Sherk, Mulligan, & Kim, 1997).

Primates: In primates, electrophysiological recordings have indicated that area middle temporal (MT) has cells that are tuned for direction and speed of a moving visual stimulus (Albright, 1984. 1989; Lagae, Raiguel, & Orban, 1993; Mikami, Newsome, & Wurtz, 1986 a, b).

Recordings have shown that the neurons in the medial superior temporal (MST) area that receives connections from the MT area have large receptive fields and are tuned to detect direction and the speed of moving stimuli (Tanaka, Sugita, Moriya, & Saito, 1993; Saito, Yukie, Tanaka, Hikosaka, Fukuda, & Iwai, 1986). Further, it has been determined that MST neurons respond specifically to optic flow stimulation showing forward or backward motion (Duffy, 1998; Duffy & Wurtz, 1991a, b; Lagae, Maes, Raiguel, Xiao, & Orban, 1994; Saito et al. 1986; Steinmatz, Motter, Duffy & Mountcastle, 1987; Tanaka, Hikosaka, Saito, Yukie, Fukada, & Iwai, 1986; Tanaka & Saito, 1989). In an interesting study, Britten and van Wezel (1998) showed that electrical microstimulation of MST neurons in monkeys trained in a heading discrimination task could lead to a change in judgement of heading, showing that these neurons are involved directly in the processing of optic flow.

Another primate area that receives output from area MT is the ventral intraparietal area (VIP) (Maunsell & Van Essen, 1983; Ungerleider & Desimone, 1986) and research has shown that this area is also involved in the processing of self-motion information and optic flow stimuli (Bremmer, Duhamel, Ben Hamed, & Graf, 1995; Schaafsma & Duysens, 1996; Schaafsma, Duysens & Gielen, 1997). Further, keeping with the dorsal stream in macaques, area 7a in the parietal cortex receives feed-forward connections from areas MST and VIP (Bremmer, Duhamel, Ben Hamed, & Graf, 2000), and neurons in this area have been shown to be involved in processing optic flow stimuli (Read & Siegel, 1997; Siegel & Read, 1997).

In primates, processing of optic flow information is not restricted to purely the dorsal stream. as has been seen with the response properties of neurons in the anterior parts of the temporal cortex. The anterior superior temporal polysensory area (STPa) receives connections from area TEO and areas MST and 7a (Bremmer et al., 2000) from the ventral and dorsal streams, respectively. Anderson and Siegel (1999) found neurons sensitive to optic flow information in the STPa area, and since a large number of neurons in this area responded to radial motion in the forward direction they propose that this area might be specialized for processing looming stimuli.

Rodents:

Although it is well established that optic flow stimuli are processed in various visual areas in cats and primates, much less work has been done in rodents. Paolini, Freeling, and Sereno (1995) have found areas lateral to V2 and V3 (areas ML and L) in the ground squirrel that may be implicated in motion processing and optic flow. Cudmore, Ellard, and Long (1995) have shown two areas in the gerbil cortex, adjacent to primary visual cortex, which they suggest may be analogous to area TP in the squirrel, and may play a role in motion processing.

5. Probing the neural substrates

Early studies of the visual control of movement in rodents have largely concentrated on subcortical sites rather than the cortex, because the role of the superior colliculus in the initiation of eye and head movements had been recognized in cats and monkeys. This emphasis of subcortical processing was largely due to the earlier belief that vision provides the animal with a perceptual representation of the external world, and the cortex plays a role in processing this representation. Over the past few years there has been a growing emphasis on recognizing the fact that vision is not merely used to "see" the world, but it plays an important role in guiding action in the external world (Goodale & Carey, 1990). Much research has shown that the cerebral cortex plays an important role in the control of visuomotor behaviour by modulating the functions of the phylogenetically older retinofugal pathway (Goodale & Carey, 1990).

Schneider (1969) suggested a functional dichotomy of the visual system into a retinotectal system and a geniculostriate system, which processes localization of stimulus and stimulus identification, respectively. Though his classification was very influential in trying to make sense of the visual system's organization, it does not take into account the role that vision plays in modulating action in the environment. Although in cats and primates, the role of eye and head movements may help identify a localized stimulus, in afoveate animals like rodents it is likely that the role of shifting of gaze through head movements is for acting on some stimulus, either orienting to it, or picking it up, etc (Goodale & Carey, 1990). A number of studies since Schneider's (1969) have shown considerable sparing of visual behaviour after lesions of the superior colliculus, indicating that the visual cortex or other subcortical structures are sufficient to mediate orientation movements (Mlinar & Goodale, 1984; Mohler & Wurtz, 1977; Schiller, True, & Conway, 1980).

Because visually guided locomotion is a complex behaviour and involves the use of many subsets of behaviour, it is not simple to specify the neural substrates involved.

Although electrophysiological studies have detected a large number of cells responsive to motion and optic flow in the visual cortex, little is understood about particular areas that modulate visually guided locomotion. Lesion studies of different cortical areas in the gerbil can indicate their involvement in the use of t-t-c, and on visually guided locomotion in general.

a. The role of the visual cortex

Rats with large lesions of visual cortex were severely impaired in their pattern discrimination ability, with permanent deficits in visual acuity (Dean, 1990). A number of studies have shown that rats (Goodale, Foreman & Milner, 1978; Goodale & Murison, 1975) and gerbils (Goodale & Milner, 1982; Mlinar & Goodale, 1984) are sometimes capable of accurately locomoting toward a target after lesions of the superior colliculus, whereas in contrast animals with visual cortical lesions show deficits with central targets in this task.

Similarly, studies with monkeys have shown that although lesions of the superior colliculus resulted in some loss in saccadic eye movements, an additional lesion of cortical areas resulted in permanent loss of this ability (Mohler & Wurtz, 1977; Schiller, et al.1980). Ingle (1982) and Mlinar and Goodale (1984) found that residual abilities in making head turns to orient toward a target after lesions of the superior colliculus were completely abolished after additional striate cortex lesions in gerbils. The detrimental effects of visual cortex lesions have also been reported for other visual and spatial behaviours, as in a jumping task (Ellard, Goodale, MacLaren Scorfield, & Lawrence, 1986), anticipatory orientation toward moving targets (Ingle, Cheal, & Dizio, 1979), detection of camouflaged apertures, and circumvention of barriers (Ingle, 1981).

There is considerable evidence that lesions of the striate cortex produce deficits in contour detection in many mammals. Dean (1978) has reported that there is an increase in contour acuity thresholds in rats after lesions of the posterior cortex. Shook (1983) has pointed out that bilateral removal of area 17, though not resulting in complete blindness or a loss of responsivity to patterned light, seems to result in a variety of problems including flicker, brightness, contour and movement acuity deficits. Thus, studies in monkeys and rodents suggest that areas receiving input from the geniculostriate pathway play an important role in visuo-spatial orientation, and that damage to the visual cortex causes impairment of these behaviours.

b. The role of the extrastriate regions

There has been considerable debate over the number of separate visual processing areas in the cerebral cortex of various species of animals. It is interesting to note from an evolutionary perspective that primary visual cortex is present in all species, including eutherians, marsupials, and monotremes, and that the posterior cortex of all eutherian mammals contains multiple interconnected areas (Krubitzer, 1995, 1998). However, the exact number, borders and layout of those areas outside the primary visual cortex are still not clearly delineated in many species. The primary visual cortex (PVC) can be clearly identified in all these species on the basis of similar architectonics, presence of visuotopic maps, subcortical afferents, and neuronal properties. However, beyond the PVC this organization breaks down, as the different extrastriate regions vary considerably in these properties in the various species studied so far (Rosa & Krubitzer, 1999).

Rosa and Krubitzer (1999) have discussed the evolution of the visual cortex and the presence of different extrastriate regions in the cortex. According to them, a simple extrastriate cortex hypothesis advocates that few subdivisions were present in the peristriate cortex of early eutherians, and the newer areas developed independently later on in other mammals. The complex extrastriate cortex hypothesis, on the other hand, proposes that the elaborate extrastriate cortex with perhaps 6-8 core fields might have existed in the earliest eutherian mammals that were subsequently inherited by other mammals.

Another interesting observation (Paolini & Sereno, 1998) is the variation in the organization of visual cortical areas, between diurnal species that rely heavily on visual information and nocturnal species that rely more on non-visual sensory input. When comparing the visual cortex of diurnal squirrels with that of rats, that are mainly nocturnal, it is seen that the striate and extrastriate cortices that represent the visual areas are more extensive in the diurnal squirrel. On the other hand the whisker-barrel field that represents the somatosensory area is three times larger in the rat, as it relies more on non-visual sensory input (Paolini & Sereno, 1998). Any probing of the extrastriate regions in the gerbil, which is a crepuscular creature, can add a lot of information to our knowledge of the organization of the visual cortex in this species. Area MT has been found in all primates, and similar areas Medial lateral (ML) and Lateral (L) have been designated in the squirrel. It would be interesting to probe the function of the extrastriate areas in the gerbil, to understand if these regions have developed through homoplasy (parallel evolution) or homology (common ancestor).

Since the cytoarchitectural work of Brodmann, the occipital visual area of the cerebral cortex has generally been divided into 3 architectonic areas, the primary visual cortex (area 17), and the extrastriate areas (areas 18 and 19). Various rearrangements have been made to Brodmann's map by many researchers based on their studies with different species in later years (e.g., rat (Zilles, 1990), mouse (Caviness, 1975), and grey squirrel (Kaas, Hall & Diamond, 1978)). Some of these researchers have used different terminology than Brodmann's and there has been some variance as to the boundaries and location of the different areas. In their investigations of the number of visual areas that exist in different mammalian species, some researchers (Coogan & Burkhalter, 1993; Cusick & Lund, 1981; Montero, 1981, 1993; Olavarria & Montero, 1984, 1989; Spatz, Vogt, & Illing, 1991; Thomas & Espinoza, 1987; Van Essen, 1979) assert that the visual cortex is organized into many distinct areas, while others (Kaas, Krubitzer, Johanson, 1989; Malach, 1989) have delineated the extrastriate cortex as a single global map of cortex surrounding primary visual cortex.

Montero (1981) investigated the visual cortex electrophysiologically and found that visual field areas stimulated in a single restricted photic stimulation study are represented in multiple cortical regions outside of primary visual cortex in the extrastriate regions. He identified six different extrastriate areas based on different retinotopic arrangements: area posterior (P), area posterolateral (PL), area laterolateral (LL), area lateromedial (LM), area anterolateral (AL), and area anteromedial (AM). Espinoza and Thomas (1983) investigated the retinotopic organization of the primary visual cortex and extrastriate areas in the hooded rat and confirmed Montero's findings. They found two additional areas in extrastriate cortex (laterointermediate and posteromedial).

Further evidence for the organization of visual cortical areas came from tracing the cortico-cortical connections between primary visual cortex and extrastriate areas. Sanderson, Dreher, and Gayer (1991) used horseradish peroxidase (HRP) histochemistry and observed that in the rat, visual cortex areas AM, PM, AL, and LM received ipsilateral input from primary visual cortex. Other HRP studies in rats (Olavarria & Montero, 1981) and guinea pigs (Spatz et al., 1991) confirmed the existence of multiple extrastriate visual areas mentioned in the electrophysiological studies of Montero (1981). Montero (1993) further investigated the retinotopy of primary visual cortex-extrastriate connections in the rat by injecting various fluorescent tracers into retinotopically different regions of the primary visual cortex and found ten different extrastriate areas with retinotopically organized connections to the primary visual area. Coogan and Burkhalter (1990) have provided support for the existence of multiple visual areas by investigating the types of reciprocal connections that might exist between these areas. They found that the primary visual cortex is bordered by several distinct areas, which they referred to as the far lateral complex (FLX), the anterior complex (AX), the medial complex (MX), and the posterior complex (PX) (Coogan & Burkhalter, 1993).

Other researchers contend that mammals such as rodents, which have poorly developed visual systems, are unlikely to have specialized multiple visual areas. They do agree that separate areas are present, but doubt the presence of many multiple specialized areas. Researchers have observed three separate retinotopic maps of the visual field, the primary visual cortex, an area lateral to area 17, and another area medial to area 17 in the occipital cortex of the golden hamster (Tiao & Blakemore, 1976) and the guinea pig (Choudhury, 1978). Benevento and Ebner (1971) found that cortico-cortical connections from primary visual cortex to extrastriate regions occurred between nearby sites rather than distant sites in opossums, and they suggest that the organization of the visual cortex is a single, global map.

Work with gerbils by Cudmore (1995) using tracers did not reveal the number of distinct visual areas reported by Montero (1993) and others, but cortico-cortical connections between PVC and extrastriate regions were consistent with results shown by Montero (1981) and Espinoza and Thomas (1983). Cudmore (1995) identified two lateral areas and one medial area in the extrastriate regions of the visual cortex, demonstrating that the gerbil visual cortex is not organized as a single global area.

Thus, while it is clear that the visual cortex plays an important role in visual behaviour not enough is known about the role of the primary visual cortex and the extrastriate areas in processing optic flow information and t-t-c, and the following studies addresses this.

Rationale for the present investigation

The concept of the use of t-t-c is interesting in that it makes sense for animals to be able to use readily available information from the environment to modulate their actions on a day-to-day basis. The review of the t-t-c literature has indicated that very few of the studies have tried to show how animals directly use t-t-c for visually guided tasks. Although Gibson's ideas were largely theoretical, his concepts paved the way for physiological investigations into the neural substrates controlling the use of t-t-c and optic flow. Review of the available literature indicates that although the use of t-t-c has been done in some species, it is important to study the empirical and physiological basis of its use in varied species.

EXPERIMENT 1

Many of the animal studies conducted in the past to study the use of t-t-c and optic flow have been naturalistic observations. However, lack of control in naturalistic observations undermine their usefulness, as it is difficult to rule out the role of other visual and non-visual cues in deceleration, or to specify the role of t-t-c in deceleration. Wann (1996), in his review of studies specifying the use of the tau and t-t-c, points out that t-t-c is not the only source of information used by animals and humans to control their movement. It is possible that animals are using a fixed proportion of their velocity before initiating deceleration. As pointed out earlier in the introduction, he also contends that there is a dearth of evidence for its use in natural situations, as the studies have biased sampling.

Generally, approaches to the guidance of locomotion using Gibson's proposal have investigated the phenomenon using both stationary observers and stationary stimuli (Schiff & Detwiler, 1979) or moving visual stimuli that were presented to static observers (Borst & Bahde, 1987, 1988). These studies do not address the different situations that can arise in the natural environment. Often, the observer is stationary while the target is moving, or the observer can be moving while the target is stationary, or both the observer and target can be moving. Studies using both static observers and static stimuli do not provide information about how t-t-c is really used in natural locomotion, when size, distance and, velocity

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Note: Experiments 1-3 reported in this thesis have been published in:

Shankar, S., & Ellard, C. (2000). Visually guided locomotion and computation of time-to-collision in the Mongolian gerbil (Meriones unguiculatus): the effects of frontal and visual cortical lesions. Behavioural Brain Research, 108, 21-37.

information is available. Studies that use static observers and moving stimuli, while providing a real flow pattern, are quite different from that result when the subject is moving and the target is stationary or both are moving.

Sun (1991) has pointed out that, although discrete behaviours like extension of the feet (Davies, 1990) or streamlining of the wing (Lee & Reddish, 1981) have been used to study the use of t-t-c, the relative velocity within a locomotory movement may be a more useful variable to pinpoint the role of t-t-c. Lee (1976) suggested that when an animal runs toward a target it would use visual cues to continually modify its locomotion. Therefore, the trajectory of an animal's movement, especially its rate of deceleration, could indicate the type of information being derived from the optic flow field. If the animals are using tau to guide their actions, the deceleration or landing should be triggered when tau reaches a threshold value.

The first experiment was a replication and extension of the findings of Sun et al. (1992), and as such, it was hypothesized that expansion of the retinal image of an increasing target should lead to an earlier deceleration, and that of a decreasing target should lead to later deceleration. Despite the success of Sun et al. (1992) in demonstrating that target changes could modulate running speed, the magnitude of the effect seen in their experiment was considerably smaller than that predicted if the gerbils were only using t-t-c information. The small effects may have been a consequence of the fact that Sun et al.'s apparatus did not allow for moment-to-moment modulation of target size in accord with the gerbil's position in the runway, as would be the case with a true "virtual" target. Another reason could be the use of extraneous cues by the animals to aid their run. Using a modified runway setup in which the change in size of the target was yoked to the animal's movement, and the setup was more rigorously controlled to eliminate extraneous cues, I predicted that the magnitude of the effect of use of t-t-c would be larger in this experiment.

Method

Subjects

Ten female Mongolian gerbils (*Meriones unguiculatus*) approximately 7-8 months old, raised in a breeding colony at the University of Waterloo, were used as subjects. The gerbils were housed individually from the beginning of the training period in standard polypropylene cages in a colony room. During training and testing, the gerbils had ad lib access to water and were food-restricted to maintain about 85% of their free-feeding weight. The gerbils were maintained on a 12:12 hour light-dark schedule and all training and testing was done during the light phase. Animal care standards set by the Canadian Council on Animal Care were strictly followed.

Apparatus

The runway used in the study was a modification of the apparatus used by Sun et al. (1992) (See Figure 1). It consisted of a 220-cm long, 20-cm wide and 25-cm high black box, with a computer monitor (Microscan 4G ADI, 14" monitor) at one end. All efforts were made to increase the visibility of the target circle and eliminate other visual cues from the setting. The inside of the runway was painted a flat black, and the monitor had an UV filter covering it to minimize reflection of light. To avoid texture and contour cues, a black cloth was used to cover the edges of the computer monitor. The runway was covered on top, such

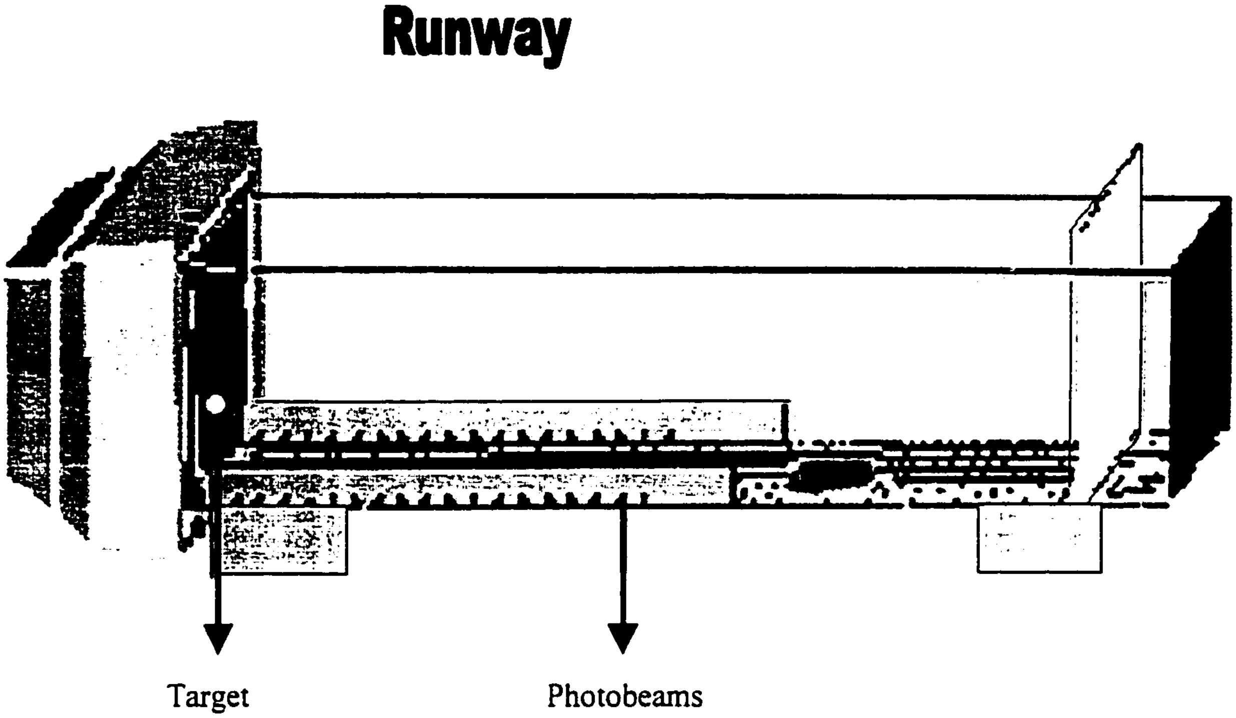

Figure 1. A drawing of the runway used in all the experiments.

that the animal had only the target to use as a guide in locomotion. Although it is, of course, impossible to present a light target with absolutely no reflected light in the chamber, every effort was made to choose a target illumination that would be within the detectable range for a gerbil but that would minimize reflection on the walls. The luminance of the target was 9.8 cd/m^2 and that of the background screen was 2.2 cd/m^2 giving a brightness contrast value of 64%.

Sun et al.'s (1992) setup had only one infrared beam at 70 cm in front of the target screen, whereas in our setup 19 infrared photobeams intersected the runway. The photobeams, starting at 95.5 cm from the computer screen, were spaced approximately 5 cm apart. Minor variations in inter-sensor distances that resulted from machining errors in the runway (in the order of 2-3 mm) were corrected for in the software that computed running velocities and target-size changes. The photobeams were positioned to track the latter part of the velocity profile of the animal's movement. The animals were trained to run to a target stimulus, a high-contrast solid white circle on the computer monitor. The software allowed for three kinds of targets in the setup: expanding probe targets, contracting probe targets and static targets. Table 1 gives the visual angles for the various types of targets from the different start positions.

Table 1. Size and visual angles for the different types of targets from the different start positions.

Target	**Diameter of the target (in cm)**	**Starting Distance (in cm)**	**Visual angle**
Expanding target & Static matched to expanding target	4.0	140-200	$1.64^\circ - 1.15^\circ$
Contracting target & Static matched to contracting target	3.5	140-200	$1.43^\circ - 1.00^\circ$
Normal Static target	2.3	140-200	$0.94^\circ - 0.66^\circ$
Normal Static target	4.3	140-200	$1.76^\circ - 1.23^\circ$
Normal Static target	5.3	140-200	$2.17^\circ - 1.52^\circ$

For the two probe trials, the tripping of the first photobeam (95.5 cm from the target) triggered a change in the size of the target circle. Stimulus size changes were calibrated to mimic the presentation of a target that was either 10 cm in front of or behind the actual face of the monitor. That is, the software calculated the visual angle and corresponding target size that would have appeared for a real target lying 10 cm in front of or behind the actual screen surface using the formula for visual angle: $\theta = \tan^{-1}$ (real target size at trial onset/distance from screen ± 10). The static targets, which served as controls, were at the same visual angle as the expanding or contracting targets at the start of the trial, and did not change in size during the run. For expanding trials the target would increase in size from 4 cm to 8 cm, and for contracting trials it would decrease from 3.5 cm to 1.3 cm. At peak velocity of an animal's running speed (60-70 cm/s), the computer would refresh the stimulus size at a frequency of 12-14 Hz.

Because of the nature of the program that controlled stimulus size changes, there was a slight difference in the starting sizes of the expanding and contracting stimuli. This was dealt with by having a provision to match static trials for size with either the expanding trials or contracting trials. In a modification of Sun et al.'s protocol, this change in size of the target stimulus was yoked to an animal's movement through the runway. As well as tracking the movements of the animal down the runway for modulating target size, the photobeam system was also used to record velocity profiles for each animal. To help the experimenter monitor the position of the animal in the runway, a control box containing a set of small red lights was used. Each light corresponded to one of the runway sensors and the light turned off when the animal blocked the sensor.

Training

All the animals were placed on a restricted feeding schedule and then trained to run toward the stimulus target to obtain a very small piece of chow. They were removed from the runway as soon as a run was completed, and not allowed to stay for an extended time at the end, so as to minimize tactile cues that could be obtained from possible wear to the flooring near the target, and olfactory cues from urine or feces. Training consisted of 10 trials per day per animal. The starting distance of each run was randomly varied from 140 cm to 200 cm in 5 cm increments and one of 5 different sized circles (2.3, 3.5, 4.0, 4.3 and 5.3 cm) was randomly used. The gerbils were tested when they could run consistently without pausing, from a distance of 200 cm, toward the target on the computer screen. A trial was terminated when the animal passed the last sensor, located 5.5 cm in front of the monitor. Training normally took approximately three weeks.

Testing

Testing was conducted over 12 days. On any one test day the test trials consisted of 2 expanding trials, 2 contracting trials, and 4 static trials (matched for starting distance and the size of the circle with the probe trials), wherein the size of the probe stimulus increased, decreased, or remained static, respectively.

The expanding and contracting trials started randomly at one of four different starting distances (140, 160, 180, or 200 cm). The 8 test trials (2 expanding, 2 contracting and 4 matched static trails) were randomly interspersed with 12 normal static trials (in which the starting distances and size of the target varied randomly as during the training session). This was done in order to reduce the possibility of detection of the target size change, which is not caused by the animal's own movement. As in training, a trial was terminated when the gerbil passed the last beam, located 5.5 cm from the monitor. These 12 normal trials were used for randomization and were not considered for analyses. The testing protocol varied in the order of presentation of type of probes and start distance from day to day, and the order of testing of the animals was also varied randomly. At the end of the testing session each animal had been exposed to 6 expanding trials, 6 contracting trials and 12 matched static trials at each of the 4 starting distances, as well as 144 normal trials. All the animals received the same testing protocol on any day. For statistical analysis, the trials of the same type and distance were averaged.

To eliminate the possible use of olfactory cues to orient toward the food during testing, I placed the food in front of the target, randomly, only during some trials. The floor of the runway was sprayed with a disinfectant and cleaned on a regular basis between animals to remove odours.

Results

Pilot studies showed that the decelerative component of velocity profiles took place over the last nine photobeams before the computer screen (starting at about 45 cm from the face of the screen). In order to maximize the power to differentiate between different kinds of trials, statistical analysis was confined to velocities over this final segment of the runway. Because static trials were matched to the different probe trials for starting distance on any test day, difference scores were used to compare running speeds under the two probe trials. Difference scores were obtained by subtracting matched static trials from probe trials for each day. Data from the same type of trial and the same starting distance over all the days were averaged for each animal.

Difference scores were analyzed using repeated measures ANOVA (Probe x Start x Distance), in which Probe refers to the expanding or contracting trials, Start indicates the four different start distances of the runs, and Distance refers to the distance of the infrared beams from the target on the computer monitor. An alpha level of .05 was used for all statistical tests (The ANOVA table is given in Appendix B). The analysis revealed a significant main effect of Probe ($\underline{F}_{(1, 9)} = 17.83$, $\underline{p} = 0.002$), indicating that there was a difference in decelerating velocity between expanding and contracting trials (Expanding $\underline{M}=$ -5 cm/sec, $\underline{SD}= 9$, Contracting, $\underline{M}= 3$ cm/sec, $\underline{SD}= 9$) (see Figure 2). The main effects of

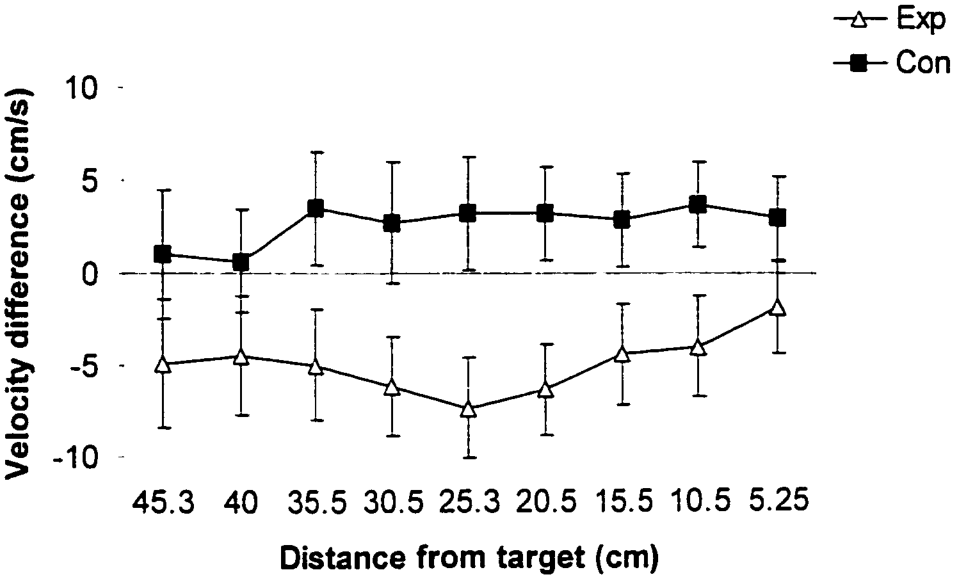

Figure 2. Line graphs showing velocity profiles (difference scores) for Expanding and Contracting trials averaged over all the start distances for all the animals over all the days. Error bars represent standard errors of the mean.

Start and Distance were found to be non-significant, and although a Probe x Distance interaction ($F_{(8, 72)} = 2.06$, $p = 0.051$) was close to significance, all other interaction effects were found to be non-significant.

The averaged velocity profiles (not difference scores) were also examined to see if the animals ran differently for the Expanding, Contracting, and Static trials (Expanding $M = 0.53$ m/sec, $SD = .09$; Contracting $M = .59$ m/sec, SD = .08; Static $M = .58$ m/sec, $SD = .08$). The velocity profiles for the three types of probes are shown in Figure 3, and although the animals ran significantly more slowly during expanding trials as compared to static ($F_{(1,9)} = 14.66$, $p = 0.004$) and contracting trials ($F_{(1,9)} = 24.61$, $p = 0.001$), the difference between probe effects for static and contracting trials was not significant ($F_{(1,9)} = 2.24$, $p = 0.169$).

The velocity profiles of individuals for expanding and contracting trials indicated considerable variability. Seven animals ran faster for contracting trials and slower for expanding trials as compared to static trials for most of their run. Two animals did not show specific probe effects in that they ran more slowly for both the probe trials as compared to static trials, but used information from the probe during the very last part of their run.

In order to see if animals were using information from the visual target, trained animals were made to run in a dark runway, with no target displayed on the screen. It was seen that all the animals were able to go to the end of the runway, but interestingly their velocity profiles were not smooth, and indicated that they stopped often and ran in small bursts (See Figure 4).

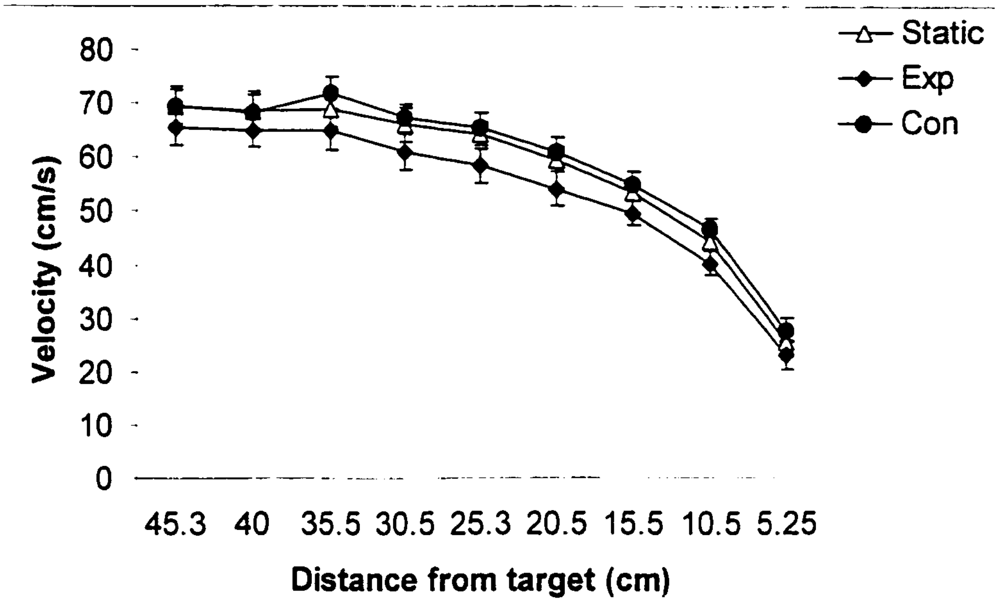

Figure 3. Line graphs showing velocity profiles for Expanding, Contracting, and Static trials averaged over all the start distances for all the animals over all the days. Error bars represent standard errors of the mean.

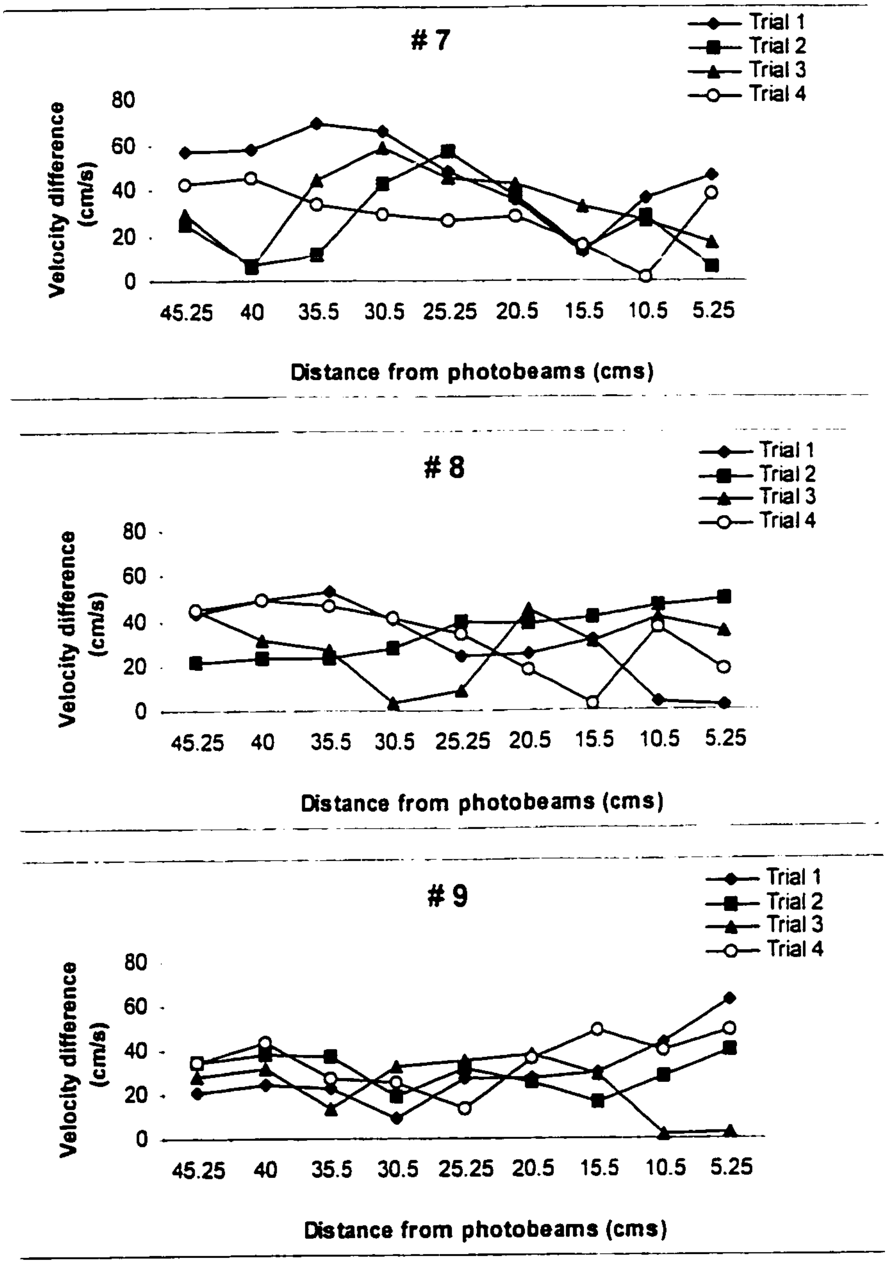

Figure 4. Line graphs showing velocity profiles for 4 trials with no targets for three individual animals.

Discussion

The results generally substantiate the hypothesis that gerbils use t-t-c information from the changing visual target to control their trajectory. They have run faster for contracting trials and have slowed down for expanding trials. Animals did not run smoothly (See Figure 4) when a visual cue was absent, indicating that in the presence of a visual cue animals use t-t-c information to modulate and aid their run. So, if visual cues are present, animals will use it to modulate their locomotion, but in the absence of visual cues, other cues will be used to complete the task.

In order to compare the effect of the changing target size on locomotion with the size of effect that would be predicted if the deceleration were to be entirely under the control of tau, a best-fitting logarithmic function (R^2=0.9654) was calculated for a deceleration curve that was derived from an average taken over all static trials for all the animals. Then, as the software that controlled the target size on probe trials had been designed to make the target appear either 10 cm in front of (expanding) or behind (contracting) the monitor, the theoretical prediction from exclusive use of tau was taken to be a shift to either the left (expanding) or the right (contracting) of the deceleration curve by 10 cm. These curves could then be used to generate theoretical difference scores. Figure 5 shows the computed theoretical difference scores, the scores obtained in this experiment, and, for comparison, the scores obtained in the study by Sun et al. (1992). The figure shows that velocity difference profiles of gerbils in the present experiment showed effect sizes that were quite comparable to those shown by Sun et al. but with slightly larger effects on expanding trials and smaller

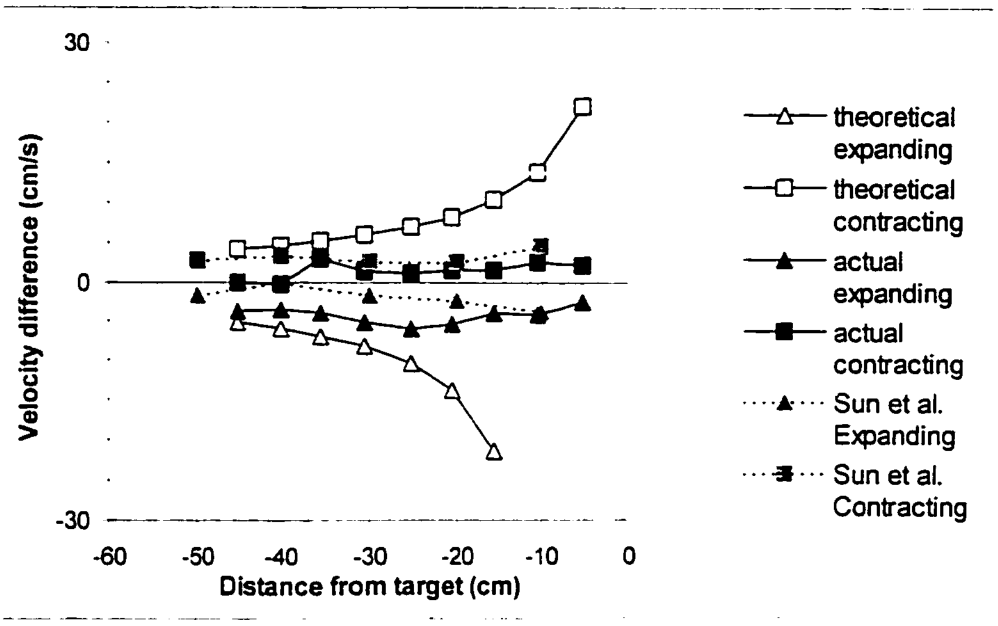

Figure 5. Line graphs showing theoretical difference scores for Expanding and Contracting trials obtained from a best-fitting logarithmic function to a deceleration curve that was derived from an average of all static trials. The equation used was $y = -0.053716+0.206725*LN (x)$. Also shown for comparison are difference scores obtained for Expanding and Contracting trials from Experiment 1, and from the Sun et al. (1992) study.

effects on contracting trials. However, the size of the effects in both experiments falls well short of theoretical prediction. Some clues that may help to account for this discrepancy come from individual differences in the velocity profiles, which were mentioned above. It is clear that although some animals modulated their running speeds in accord with the prediction, there were individual differences in the use of t-t-c information. Thus, it would seem that although the animals are using information from the optic flow to control t-t-c, it is not the sole source of information being used in the control of locomotion. Static distance cues such as stereopsis, vergence, etc., could become salient as the texture detail of the target becomes visible at close quarters near the end of the run. It is also reasonable to assume that at the very end of the run, the small amount of illumination from the target, as well as differential reflection of light from the junction of the computer screen and the walls of the runway would aid the animal's movement. Further, the animals may be using other non-visual cues like proprioceptive and vestibular information.

Expanding targets exerted a larger effect on running speed in the present setup than contracting targets. One reason for this observed difference could be a limitation of using a virtual set up. For expanding trials, the effects of modulation of deceleration should occur early before the end of the runway, and those for the contracting trials should presumably occur behind the actual target (which can't be measured of course). So, the part of the run that is being measured for the expanding effect is bigger than that for the contracting effect (See Figure 6).

A second possible reason for the apparently smaller effect of the contracting stimulus is that there may have been some trials in which the gerbils detected the size change as target

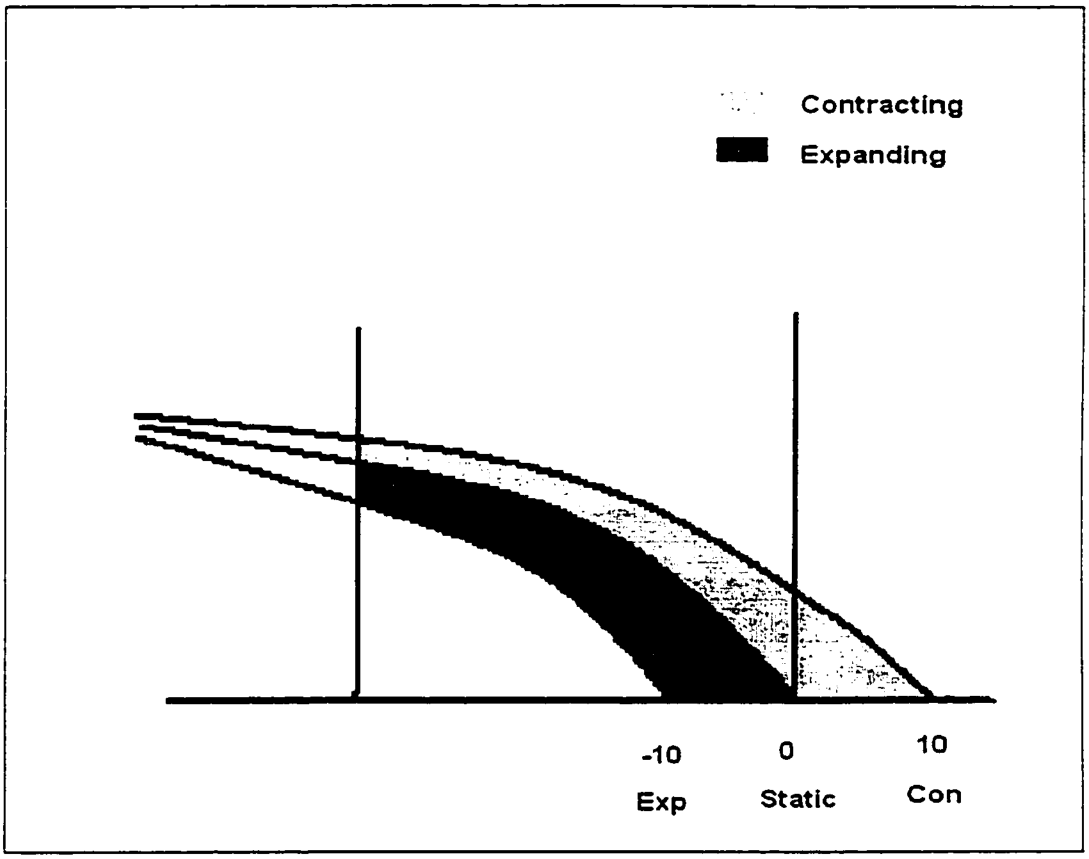

Figure 6. Hypothetical location of stopping during Expanding (-10 cm), Static (0 cm) and Contracting (10 cm) trials. Area of the curve between the Expanding trial and Static trial is larger than the area under Static trial and Contracting trial, by virtue of using a virtual target.

movement, rather than interpreting it as an effect of their own movement (which is what we had predicted). It seems reasonable to suppose that in those trials on which the animals may have detected target motion, it might well have produced hesitation. Hesitations would artificially exaggerate the predicted effects of expanding target trials and artificially minimize the effects of contracting target trials.

EXPERIMENT 2

Experiment 1 showed that gerbils use t-t-c information to modulate their locomotion during visually guided locomotion. The next aspect of the study was directed at looking at the neural basis for the use of t-t-c information. Is the use of t-t-c cortically dependent and, if so, what areas of the cortex may be involved?

Although there has been much interest in the use of vision in locomotion, little is known about the neural substrates underlying the use of retinal image information and t-t-c in locomotion. Because visually guided locomotion is a complex behaviour, it is not simple to specify the neural substrates involved. Although electrophysiological studies have detected a large number of cells responsive to whole-field motion in the visual cortex, little is understood about particular areas that modulate visually guided locomotion. Lesion studies of different cortical areas in the gerbil can indicate their involvement in the use of t-t-c and the tau variable and on visually guided locomotion in general.

Experiment 2 was conducted to study the effect of large visual cortex (VC) lesions and frontal lesions on visually guided locomotion. The frontal cortex lesion was used as a control area, to compare with the visual cortex lesion, to ensure that any effects of the lesions on the use of t-t-c could be attributed to a particular location, and not to damage to any part of the cortex per se.

A review of the literature shows that damage to the frontal cortex in rodents leads to a variety of behavioural changes. It has been shown that many species-typical behaviours are disrupted, and the performance of a variety of learning tasks is affected in the lesioned animals (Ellard, Stewart, Donaghy & Vanderwolf, 1990; Kolb & Cioe, 1996; Kolb & Nonneman, 1974; Kolb & Whishaw, 1983, Vanderwolf, Kolb & Cooley, 1978). However, Kolb (1990b) points out that although prefrontal cortex lesions affect the complete execution of species-typical behaviours, most of the components of these behaviours remain in the animal's repertoire, indicating that although organization of these behaviours is affected, their production is not.

Because the task in the present investigation involves locomotion. effects of frontal lesions on motor abilities will be briefly reviewed. Vanderwolf et al. (1978) found that neocortical lesions did not cause loss of specific movement patterns, and that walking, rearing, and climbing were all observed to be normal or almost normal in these rats. Although studies have shown impairment in many motor behaviours. Gentile. Green. Nieburgs, Schmelzer, and Stein (1978) demonstrated that removal of the frontal cortex though having an effect on some motor behaviour. did not affect locomotion in rats. Other studies in kittens and rats have shown that lesions of the frontal cortex cause increased locomotion and activity (Kolb & Gibb. 1991; Levine. Hull. Buchwald & Villablanca. 1978; Lynch. Ballantine & Campbell. 1971; Wilcott, 1979).

There has been little work done on the effect of frontal lesions on visual tasks like the one used in the present investigation, but in general, it appears that frontal lesions do not affect visual tasks significantly. Ellard and Ilkov-Moor (1995) found that animals with lesions of motor cortex were not affected in the use of distance-estimation in a jumping task, but that gerbils with lesions to anteromedial frontal cortex (AMC) had subtle deficits in a visual distance estimation task. They found that AMC lesions caused a decrease in the frequency of head bobs that gerbils normally make to gain retinal motion information (Ellard, Goodale, & Timney, 1984), and suggest that the AMC area is involved in correlating self-motion cues with retinal image movement. Mendoza and Thomas (1975) found that squirrel monkeys with frontal lesions were impaired on delayed response but were not affected on brightness discrimination. Crowne and Pathria (1982) reported that after unilateral frontal damage, rats and monkeys could detect and respond appropriately to contralateral visual stimuli signalling avoidance. In general it appears that frontal lesions in rodents at best have some subtle effects on locomotor behaviour in the animals.

Based on the literature review, it was hypothesized that large visual cortex lesions would attenuate an animal's ability to make use of visual information from the stimulus target, and have an effect on its decelerative phase during locomotion. Also, because most studies have shown that there is no effect of frontal lesions on visual or locomotor tasks, it was hypothesized that frontal lesions would not affect an animal's ability to use information from the visual target to modulate its locomotion toward a target.

Method

Subjects

Twenty Mongolian gerbils (8 males and 12 females) approximately 10-12 months of age served as subjects for Experiment 2. This experiment was conducted in two parts for ease of scheduling training, surgery and testing days. The treatment groups consisted of four shams and five VC lesioned animals, and six shams and five frontal lesioned animals, for the first and second part, respectively. Conditions for housing, care, food restriction, and training were identical to those of animals in the previous experiment.

Apparatus

The same runway used in Experiment 1 was used in this experiment.

Training

The animals were trained to run toward the target on the computer screen to obtain a food reward, in exactly the same way as in Experiment 1.

Surgery

Subjects were anaesthetized with sodium pentobarbital (Somnotol, 60 mg/kg i.p.) and administered an analgesic (Temgesic, 0.2mg/kg s.c), and atropine sulfate (0.05mg/kg. s.c), to inhibit secretions in the nose, mouth, throat, and lungs. The incision site was prepared and artificial tears were introduced in the eyes to keep them from drying out. Each animal was placed in a stereotaxic apparatus, a 1 cm midline incision was made, and the skin was retracted. At this point, the animals were randomly selected to be in either the sham group or the lesion group.

The incisions of the sham animals were sutured closed with absorbable vicryl suture material. For the animals in the visual cortex lesion group, after drilling of the skull, large visual cortex lesions were made through aspiration. Using information from Cudmore (1995), the lesions were located approximately 3 mm posterior to bregma and between 3 and 5 mm lateral to the midline and extended in a caudal direction to approximately 6 mm posterior to bregma and between 2.5 to 5 mm lateral to the midline. For the frontal lesion animals, the frontal cortex was exposed by drilling a small hole anterior to the bregmoidal junction and lateral to the midline, and the exposed cortex was removed through suction aspiration (Ellard & Goodale, 1986; Ellard & Ilkov-Moor, 1995). Following lesions, the damaged area was covered with a small piece of Gelfoam to control bleeding and the area was flushed with isotonic saline. The wound was sutured closed. All animals were placed on a heating pad and given 1-2 cc of Ringer's lactate solution for rehydration subcutaneously, and a respiratory stimulant (Dopram, 5mg/kg of body weight, s.c) to promote speedy and safe recovery from anaesthesia. They were monitored closely until ambulatory and returned to their home cages. The gerbils were allowed a period of 7 days of recovery before testing.

Testing

The animals were tested for 6 days using the same procedure as in Experiment 1. As mentioned earlier, this experiment was conducted in two parts. We first looked at the effects of large visual cortex lesions on the use of optic flow information, and in order to ascertain that results obtained from the visual cortex lesions were not merely a non-specific effect of damage to the cortex per se, the second part of the experiment was designed to evaluate the effect of frontal lesions on the use of optic flow during locomotion.

Histology

At the conclusion of testing, the animals were deeply anaesthetized with sodium pentobarbital (Euthanyl, 240 mg/kg, i.p), and perfused intracardially with isotonic saline and buffered 10% formalin. Their brains were extracted and fixed in formalin for 24 hours. The brains were removed from formalin, washed in distilled water and immersed in 10 % sucrose-phosphate solution for 24 hours for cryo protection. The brains were then embedded in gelatin and immersed in formalin for 48 hours. They were frozen and sectioned at 40 μm on a sliding microtome. Every fourth section was mounted on slides coated with gelatin. The slides were stained with metachromatic thionin and cover-slipped. The images of the brain sections were loaded onto the computer using a black and white CCD camera (Panasonic CCTV, Model WV-BL200). The brain sections were reconstructed using the Image PC program (Scion Corporation), where 2D images can be organized and stacked as a 3D array. The stack thus consists of individual slices that can be examined one by one. Tissue damage on each slice was identified and marked by outlining the area of lesion.

Results

Anatomical Results

Figure 7 shows a representative reconstruction of a visual cortex lesion, and for comparison purposes, a reconstruction of the visual cortex areas of a gerbil brain from Shook (1983). Estimates of visual cortical areas were made using information and cytoarchitectonic maps from various sources (Caviness, 1975; Cudmore, 1995; Loskota, Lomax & Verity, 1974; Shook, 1983). The visual cortex lesions were large in all the animals and included the primary visual cortex and medial extrastriate regions in all five of the animals. The lateral extrastriate region was not consistently damaged in both hemispheres for all the animals. The lesions extended into parietal cortex in most of the animals. In four of the animals, there was some sparing of the occipital pole area, either in both hemispheres or in one of the hemispheres. Subcortical damage in the lesioned brain was determined by microscopically examining slices, and counting cells and noting gliosis, in comparison to a normal animal's brain. Examination of the thalamus revealed cell loss in the lateral geniculate

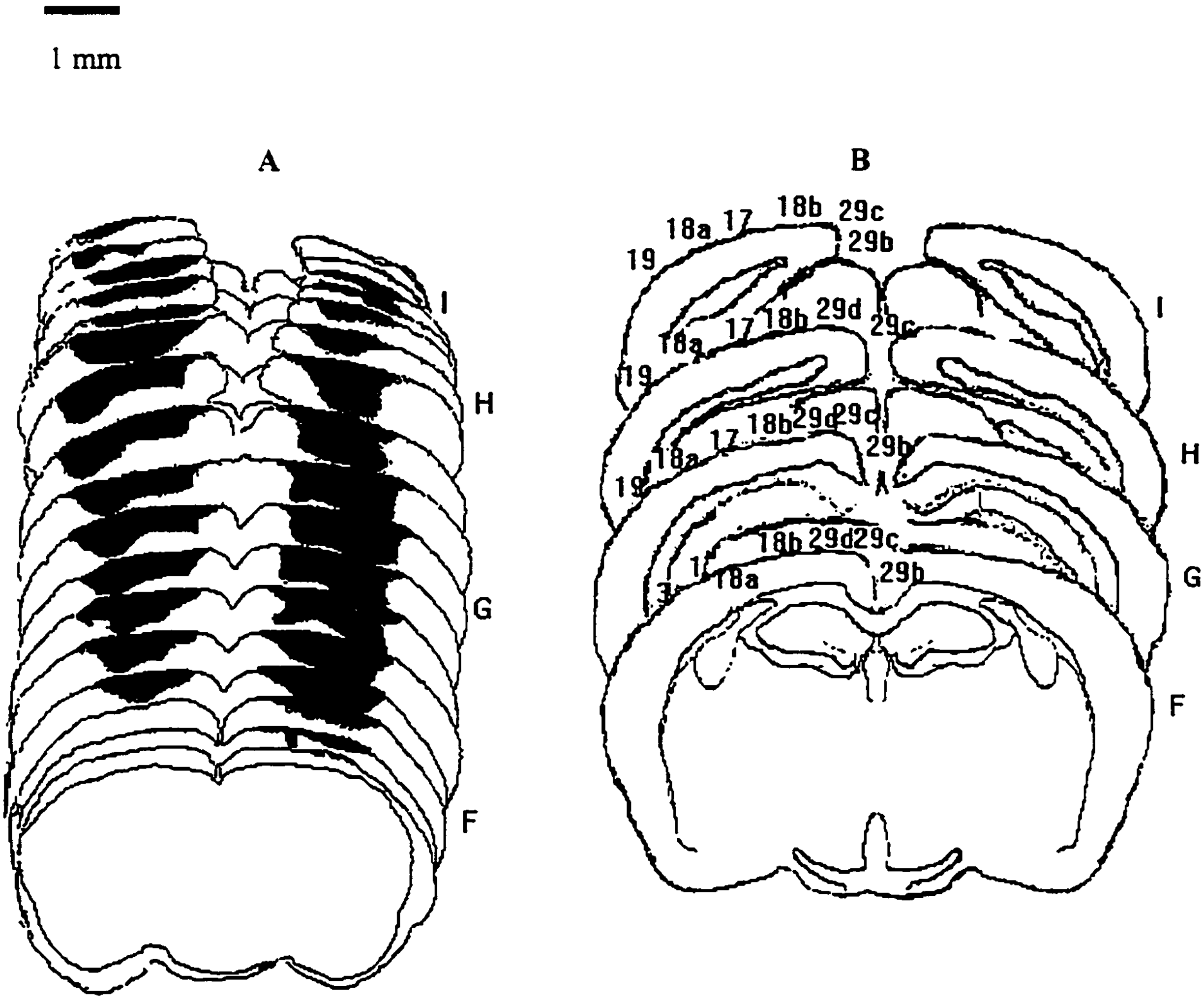

Figure 7. Schematic representation of A) a reconstruction of a representative visual cortex lesion and for comparison purposes B) shows some of the visual cortex locations of a gerbil brain, adapted from Shook (1983).

nucleus in these animals, confirming the cortical damage to the visual cortical areas. Diffuse cell loss in the lateral posterior nucleus was also observed in some of the animals.

Figure 8 shows a representative frontal cortical lesion, and for comparison purposes a reconstruction of frontal cortical areas of a gerbil brain from Shook (1983). For the frontal group, two animals had damage to the frontal cortex (area 6) and some parts of anteromedial cortex (area 8). For one of these animals, some parts of cingulate cortex were damaged, and there was encroachment on areas 4 and 3a in the right hemisphere. For another two of the frontal animals, damage was largely restricted to area 6 and mainly the motor cortex. For the last animal, the lesion in the right hemisphere was small and affected only the motor rtex, whereas damage to the left hemisphere extended into the parietal area and destroyed large areas of motor and somatosensory cortex. All the lesions were cortical, and subcortical structures were not subject to direct damage. There was some cell loss and gliosis evident in the ventromedial nucleus for three of the animals, but no clear pattern of degeneration in the other two animals.

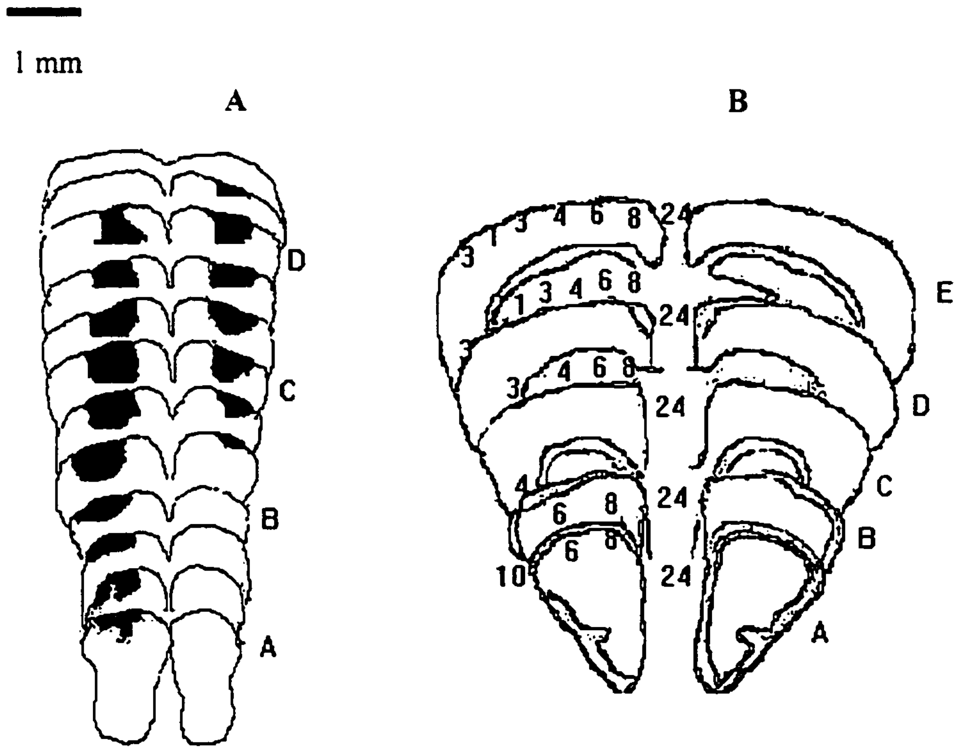

Figure 8. Schematic representation of A) a reconstruction of a representative frontal lesion and for comparison purposes B) shows some of the frontal areas of a gerbil brain, adapted from Shook (1983).

Behavioural Results

Data from both parts of this experiment were combined to get three treatment groups: Shams (N=10), Visual Cortex lesions (N=5) and Frontal lesions (N=5).

In order to rule out the possibility that the cortical lesions produced basic differences in velocity profiles, we compared the static trials of the sham and lesioned animals over the four starting distances. There was no significant difference in static trials over all the days for sham and lesion animals (Treatment- $\underline{F}_{(2,17)} = 0.40$, $\underline{p} = .674$; Treatment x Distance- $\underline{F}_{(16,136)} = 1.53$, $\underline{p} = .098$) indicating that the animals from the three treatment groups were running comparably in the runway when the target was static. A main effect of Distance was found to be significant, ($\underline{F}_{(8,136)} = 225.5$, $\underline{p} < .01$), which is to be expected, as the animals would slow down as they reach the end of the runway.

As in Experiment 1, the velocity profiles from the last nine photobeams were used for analysis and difference scores between the probe and the control trials were used to assess the change in velocity profile over the Expanding and Contracting trials. Data from trials of the same type and starting distance were averaged. A 4-way mixed ANOVA, with one between-group factor (Treatment: shams, VC lesions, frontal lesions), and 3 within-group factors (Probe: Expanding vs. Contracting trials, Start: the starting distance of each run, and Distance: the distance of the photobeams from the target along the runway), was conducted. Appendix C gives the ANOVA table for velocity difference scores. A significant 3-way interaction (Treatment x Probe x Distance; $\underline{F}_{(16,136)} = 2.59$, $\underline{p} = .002$) indicated that there was an effect of the different probes at different distances from the target, depending on the treatment groups (see Figure 9). Main effects of Probe ($\underline{F}_{(1,17)} = 13.81$, $\underline{p} = .002$) and

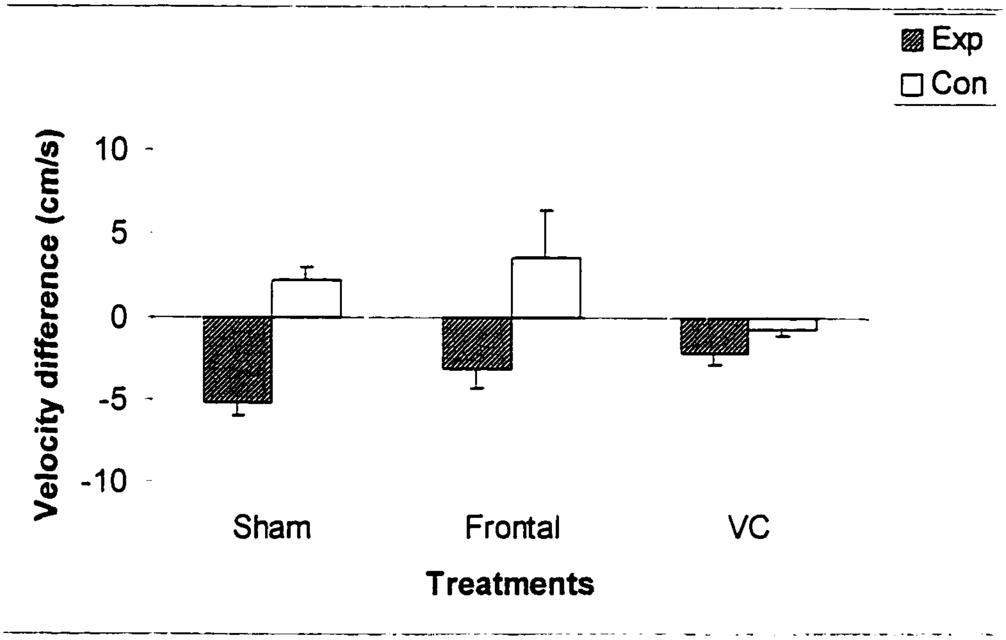

Figure 9. Bar graph showing difference scores for Expanding and Contracting trials for the Shams, Visual cortex (VC), and Frontal lesioned animals. Error bars represent standard error of the mean.

Distance ($\underline{F}_{(8,136)} = 3.43$, $\underline{p} = .001$) were also found to be significant, and were qualified by the significant 3-way interaction. No other main effects or interaction effects were found significant.

We decomposed the significant interaction effect by looking at treatment effects over the two different probes separately (See Figure 10). There was a significant main effect of Treatment ($\underline{F}_{(2,17)} = 3.59$, $\underline{p} = .05$) for Expanding trials, indicating that animals from different treatment groups reacted differently to the expanding probes. For Contracting trials there was a significant Treatment x Distance interaction effect ($\underline{F}_{(16,136)} = 2.05$, $\underline{p} = .014$), indicating that animals from the different treatments reacted differently to the Contracting trials at different distances along the runway. Comparing individual treatments, we found a significant difference in the effects of Expanding trials between Shams and VC animals ($\underline{F}_{(8,104)} = 2.40$, $\underline{p} = .02$), while no treatment effects were significant between Shams and Frontals, or Frontals and VC animals. For Contracting velocity difference scores we found that Shams differed from VC animals ($\underline{F}_{(1,13)} = 5.40$, $\underline{p} = .037$), and Shams differed from Frontals in their runs at different parts of the runway ($\underline{F}_{(8,104)} = 2.59$, $\underline{p} = .013$), whereas Frontals did not differ from VCs for Contracting velocity difference scores.

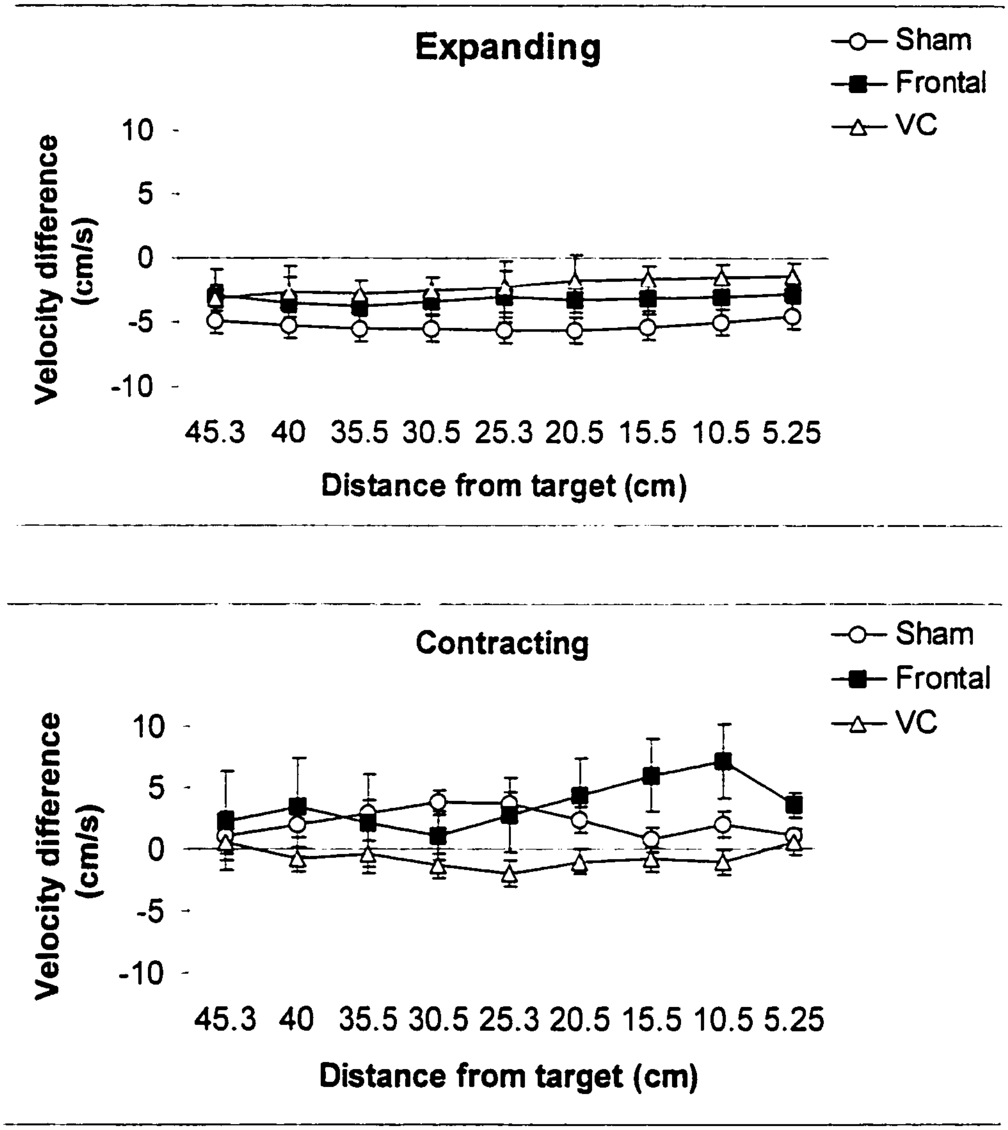

Figure 10. Line graphs showing velocity profiles (difference scores) and Standard error of means for animals from Sham, Visual Cortex (VC), and Frontal treatments for Expanding and Contracting probe trials. Separate axes are used to show the two different probes.

Thus, our results show that VC animals are affected for both Expanding and Contracting trials as compared to Shams, whereas frontal animals are more affected for Contracting trials than for Expanding trials as compared to Shams.

Discussion

The results from this experiment indicate that there is an effect of the change in size of the probe targets on the animals' locomotion at different parts of the runway, based on their treatment group. From Figures 8 and 9, it can be seen that Sham animals used information from the changing size of the stimulus on their retina to modulate their deceleration during runs, thus replicating the finding from Experiment 1. There was no evidence for a probe effect for the VC lesioned animals, indicating that visual cortex lesions attenuated their ability to use information from the visual target to modulate their locomotion. The effects of probe trials were altered in Frontal animals, but the pattern of differences was somewhat different to that seen in the VC group.

In Experiment 1, it was suggested that animals use a combination of t-t-c information and other cues, such as looming, luminance, etc., to modulate their locomotion. Animals with lesions to visual cortex appeared not to be affected by changing target size on probe trials, suggesting that visual cortex is involved in some aspect of processing motion information to guide locomotion. This finding corroborates evidence for involvement of visual cortex in certain visually guided tasks in rodents (Dean, 1990; Ellard & Goodale, 1986; Goodale et al., 1978; Ingle et al., 1979; Shook, 1983). On the other hand, it was obvious that gerbils with visual cortex lesions were not totally lacking information regarding the location of the target. If they had been, one would expect to see velocity profiles like those shown in Experiment I for animals that had no target. In a jumping task, Carey, Goodale, and Sprowl (1990) found that Mongolian gerbils with large bilateral lesions of the visual cortex were still able to use static retinal image size as a source of distance information. The animals in the present study did not show the sparing of effect shown by the gerbils in the Carey et al., (1990) study, presumably because of the addition of the motion component to the runway task. No gerbil in any group, for instance, made physical contact with the monitor at the end of the runway. Indeed, velocity profiles for animals with cortical lesions were, on average, not severely affected by the lesions. This indicates that the lesions in the present study have impaired one form of visual motion processing, the use of t-t-c, while leaving intact other uses of vision.

The effects of frontal lesions on runway performance were somewhat surprising. Initially, the intent in including this group had been to provide a cortical lesion control group in which it was not predicted that the lesions would have an effect on modulation of running speed on probe trials. Instead, the pattern of results suggests that, compared to shams, frontal animals showed smaller probe effects on expanding trials and, though not significant, slightly larger probe effects on contracting trials. In other words, there is some suggestion in the data shown in Figure 9 that all probe effects for frontal animals have shifted upwards. In light of the earlier discussion of the possibility that gerbils might, on some trials, be detecting the target size change as though the target itself were moving, it is possible that the effect of the frontal lesions might have been to render the animals unable to detect target size changes that might have occurred in some trials in normal animals, while leaving intact the modulation of running speed on the basis of the false t-t-c feedback produced by the virtual targets. This possibility was tested further in Experiment 4 and will be discussed later.

Two animals in the frontal group had damage to the anteromedial cortex (AMC), which may have caused different difficulties as compared to the other lesioned animals. Teuber and Mishkin (1954) suggested that the frontal eye field, the primate homolog of AMC, participates in coordinating movements of the visual field with self-motion. Behavioural and electrophysiological evidence has also verified that the AMC is a site for generation of head movements that aid in distance estimation (Bizzi & Schiller, 1970; Bossom, 1965; Ellard & Ilkov-Moor, 1995, Sinnamon & Galer, 1984). It is possible that the runs of these animals reflected the loss of ability to use cues from self-motion and depth vision.

EXPERIMENT 3

In Experiment 2, the effect of large visual cortex lesions on the use of t-t-c was explored to see cortical involvement. Having found that such lesions attenuate an animal's ability to use information from the visual target, it was next decided to investigate different areas of the visual cortex to see if any specific region of the visual area controlled the use of the t-t-c variable.

The research reported here employed Mongolian gerbils, which are visual animals and use a variety of visual behaviours. As reviewed earlier in the introduction, the visual cortex in rodents subserves many visual functions. Although more work needs to be done to see if the visual areas in gerbils have differentially specialized regions, work by Cudmore (1995) identified two lateral extrastriate areas and one medial extrastriate area in the extrastriate regions of the visual cortex. Because the task used in the present investigation involves the use of t-t-c, it was decided to focus on areas in the extrastriate region that have been implicated in motion perception and the use of optic flow information (Paolini et al.,1995).

Experiment 3 was conducted to study the effect of small primary visual cortex and lateral extrastriate lesions on the use of t-t-c in locomotion. Based on previous studies (Mlinar & Goodale, 1984; Shook, 1983) that showed the involvement of the primary visual cortex in different visual tasks, it was hypothesized that V1 lesions would attenuate an animal's ability to make use of visual information from the stimulus to some extent. It was also hypothesized that lateral extrastriate lesions would affect an animal's ability to use t-t-c information, and that the effect would be more pronounced for the lateral group as this is the area where optic flow processing cells have been found in different species.

Method

Subjects

Seventeen Mongolian gerbils (10 males and 7 females) approximately 10-12 months old were used as subjects. All the conditions for housing, food restriction, training and testing were identical to those of animals in the previous experiments. The treatment groups for this experiment consisted of six shams, seven lateral lesioned animals, and four V1 lesioned animals.

Apparatus

The apparatus for this experiment was the same as that used in Experiments 1 and 2.

Training

The animals were trained to run toward the runway in exactly the same manner as for the previous study.

Surgery

Radio-frequency energy (Radionics Model RFG-4A Research RF Lesion Generator System) was used to make small focal lesions for this experiment. Animals were prepared for surgery as in Experiment 2. The animals were placed in stereotaxic earbars, and an incision was made and the skin retracted. At this point, the animals were chosen to be in either the Sham or one of the lesion groups. The incisions of the Sham animals were sutured closed. The region of the primary visual cortex region and the lateral extrastriate cortex region was determined using information from Cudmore (1995). For the V1 lesions, 2 small holes were drilled on each hemisphere, one 4 mm posterior to bregma and 4 mm lateral to the midline, and the second 6 mm posterior to bregma and 4 mm lateral to the midline. Similarly, for the Lateral extrastriate lesions, 2 small holes were drilled on each hemisphere, one 4 mm posterior to bregma and 6 mm lateral to the midline and the second 6 mm posterior to bregma and 6 mm lateral to the midline. A suture needle was inserted into the skin of the animal and wet with a few drops of saline for grounding. Then a radio-frequency electrode (0.33 mm in diameter) was carefully lowered to a depth of 0.5 mm into each of these holes. Radio-frequency current was passed through the electrode to reach a tip temperature of 70° C for 45 seconds. On completion, the incision was sutured. Post-operative care for all the sham and lesioned animals was identical to that of animals in Experiment 2.

Testing

After a period of seven days of recovery, the animals were tested for six days using the same procedure as in Experiment 2.

Histology

The animals were perfused, their brains were extracted, and histology was done following the same procedures as that of Experiment 2.

Results

Anatomical results

Figures 10 and 11 show representative reconstructions of a V1 lesion and a lateral extrastriate lesion, respectively. For the lateral group, the focal lesions of five of the seven animals were

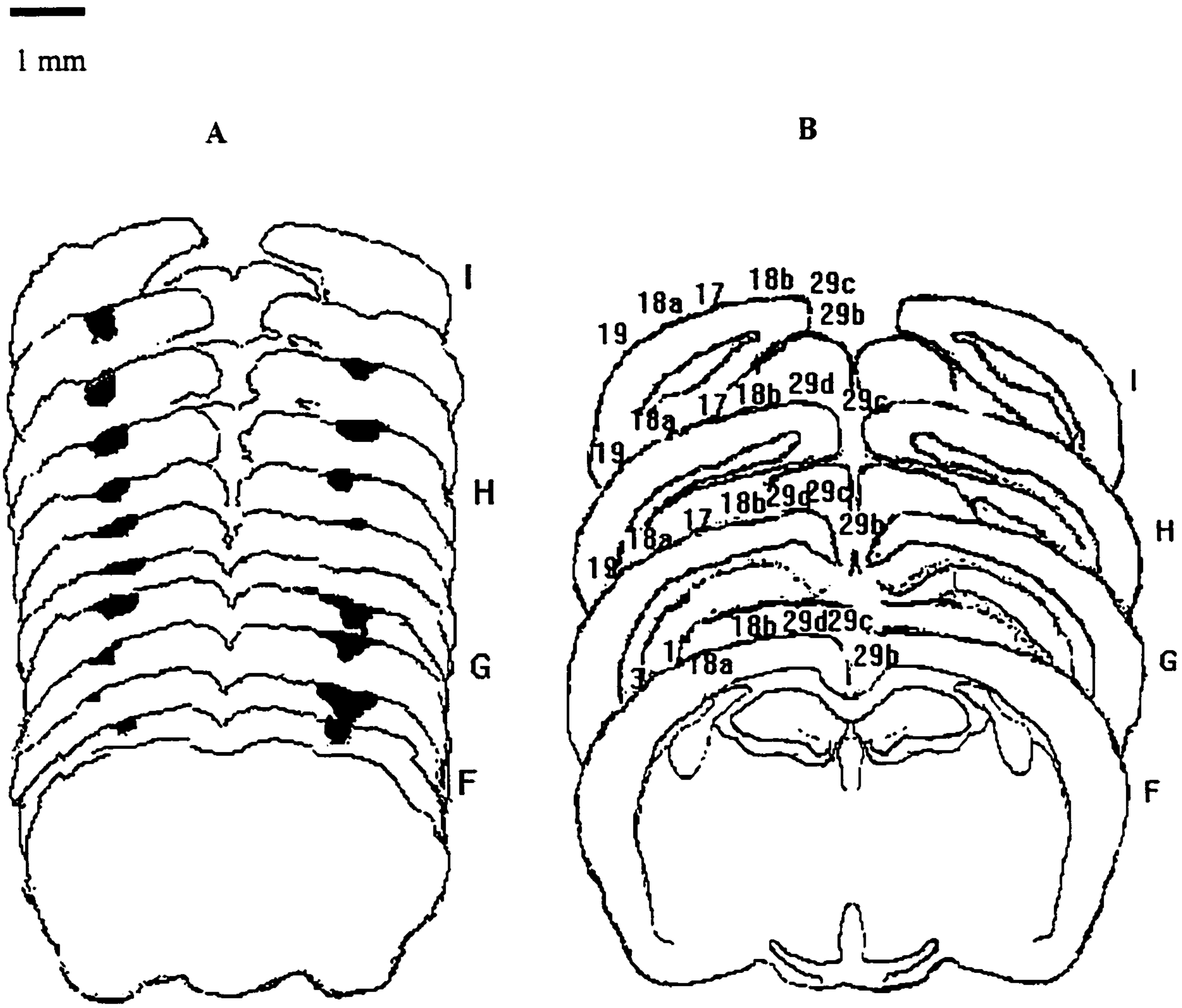

Figure 11. Schematic representation of A) reconstruction of a representative primary visual cortex lesion and B) shows some of the visual areas of a gerbil brain, adapted from Shook (1983).

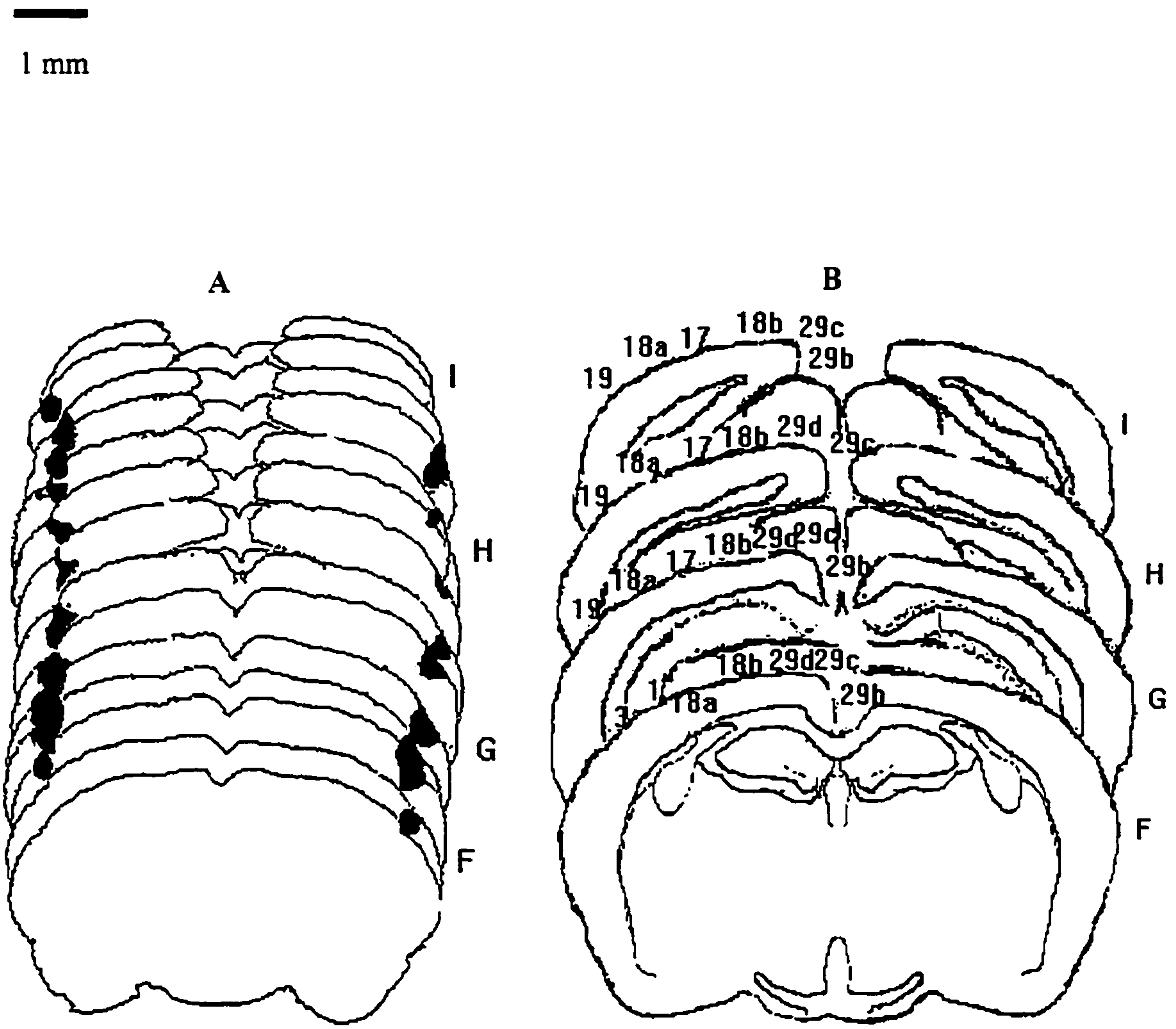

Figure 12. Schematic representation of A) reconstruction of a representative lateral extrastriate lesion and B) shows some of the visual areas of a gerbil brain, adapted from Shook (1983).

in the lateral extrastriate region, with lesions of the other two animals encroaching onto V1 in one hemisphere. The lesion on the right hemisphere of one animal was very deep and caused some callosal damage. For the V1 animals, the lesions inflicted damage on the V1 region in all animals. The lesion area in one animal was very large, and went into the medial extrastriate cortex. The lesions of three of these animals were very deep and caused callosal damage, with one of the animals having hippocampal damage as well. Subcortical damage was not very apparent, perhaps because the lesions were small and focal.

Behavioural Results

In Experiment 3, as in the previous experiment, the static trials of shams and lesioned animals were examined to see if there was any effect of the lesions on the velocity of animals. There was no significant difference in static trials over all the days for sham and lesioned animals (Treatment- $\underline{F}_{(2,14)} = 0.16$, $\underline{p} = .857$; Treatment x Distance- $\underline{F}_{(16,112)} = 1.12$, $\underline{p} = .342$), indicating that the animals from the three treatment groups were running in the same manner in the runway when the target was static. Once again a main effect of Distance ($\underline{F}_{(8,112)} = 21.56$, $\underline{p} < .01$) was found to be significant, indicating that the animals were running differently at different parts of the runway, which is to be expected.

In order to assess the change in velocity profile over the Expanding and Contracting trials, difference scores between the probe and the static trials were used as before. Treatment of data and subsequent data analyses were identical to that for Experiment 2. Appendix D gives the ANOVA table from velocity difference scores. There was a significant 2-way interaction effect (Treatment x Probe, $\underline{F}_{(2,14)} = 11.43$, $\underline{p} = .001$),

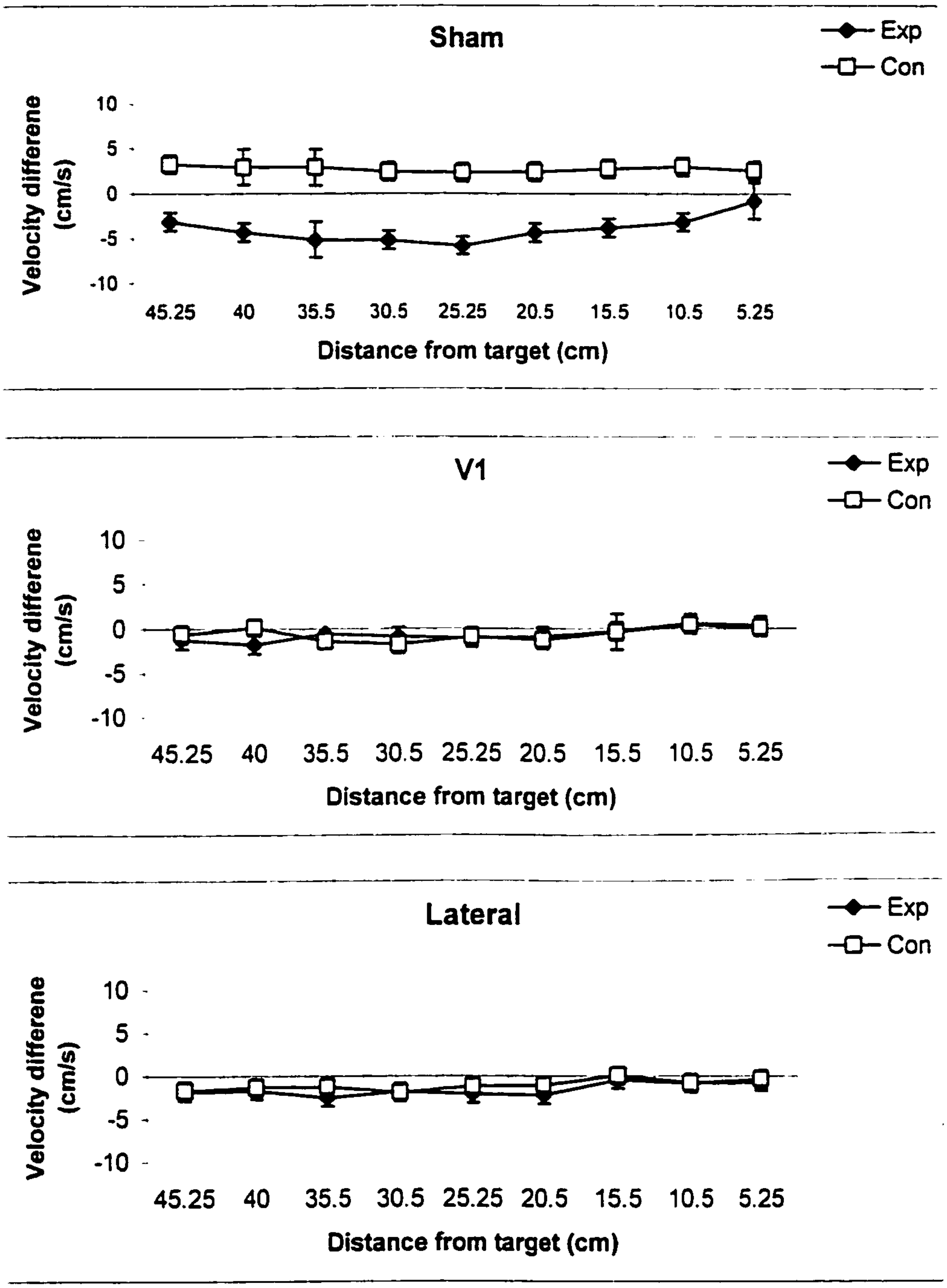

Figure 13. Line graphs showing velocity profiles (difference scores) for Expanding and Contracting trials for animals from the Sham, V1 and Lateral treatments. Error bars represent standard error of the mean.

indicating that animals from the three treatment groups reacted differently to the two probe trials (See Figure 13). A main effect of Probe ($\underline{F}_{(1,14)} = 13.42$, $\underline{p} = .003$) was also significant and was qualified by the significant 2-way interaction. Further, main effects of Start ($\underline{F}_{(3,42)} = 13.87$, $\underline{p} < .01$) and Distance ($\underline{F}_{(8,112)} = 3.51$, $\underline{p} = .001$) were also found to be significant.

The velocity difference scores for the four start distances were averaged and analyzed to understand the differential effect of the probes on animals from the three treatment conditions. For sham animals there was a significant Probe main effect ($\underline{F}_{(1,5)} = 18.78$, $\underline{p} = .007$), indicating that they were responding to the two probe targets differentially while running in the runway. For both the lesion group animals there were no differences for any main or interaction effects, which show that the animals were not using information from the changing target to modulate their locomotion.

We also looked at the effect of treatment on the two probes separately (See Figure 14). For Expanding trials there were significant main effects of Treatment ($\underline{F}_{(2,14)} = 3.85$, $\underline{p} = .047$) and Distance ($\underline{F}_{(8,112)} = 4.15$, $\underline{p} < .01$), and for Contracting trials, a main effect of Treatment was found to be significant ($\underline{F}_{(2,14)} = 10.47$, $\underline{p} = .002$).

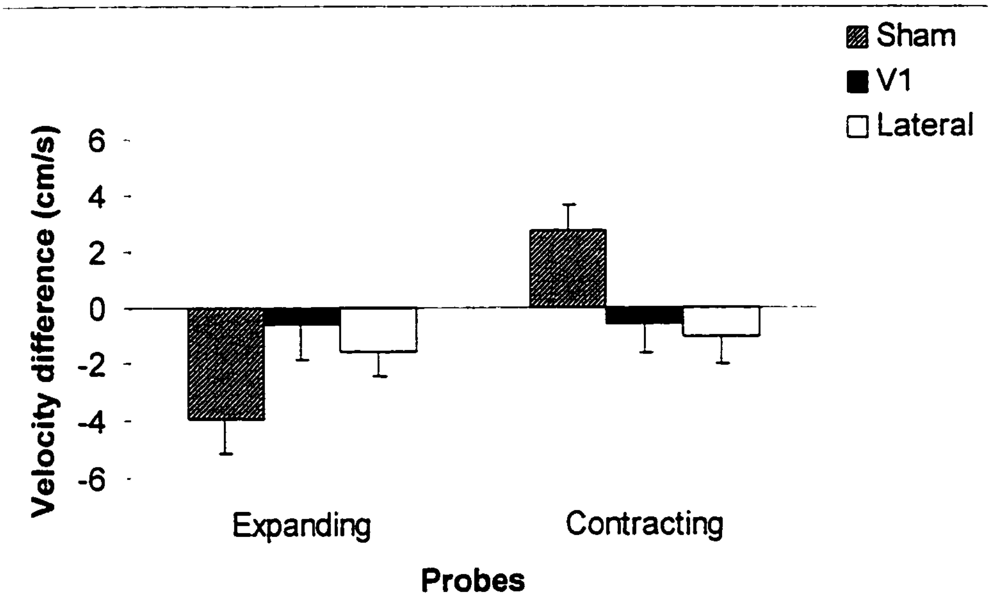

Figure 14. Bar graph showing probe effects for the Sham, V1, and Lateral treatment groups. Error bars represent standard error of the mean.

Table 2 gives the results from the breakdown of main treatment effects for the Expanding and Contracting probes.

Table 2: Effect of treatment on Velocity difference scores, for Expanding and Contracting probes separately.

Expanding trials	**Contracting trials**
Shams vs. V1s, (F $_{(1, 8)}$ = 4.50, p = .067) +	Shams vs. V1s, (F $_{(1, 8)}$ = 13.14, p = .007) *
Shams vs. Laterals, (F $_{(1, 11)}$ = 3.90, p = .074) +	Shams vs. Laterals, (F $_{(1, 11)}$ = 14.71, p = .003) *
V1s vs. Laterals (F $_{(1, 9)}$ = 1.43, p = .262) ns	V1s vs. Laterals (F $_{(1, 9)}$ = 0.15, p = .707) ns

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Note: *- significant; +- close to significance; ns- not significant

Discussion

The results from this experiment reiterate the findings of the first two experiments that sham animals use t-t-c information to modulate their locomotion in the runway. Even small lesions in the primary visual cortex and extrastriate lateral area affect an animal's ability to modulate its locomotion based on information from t-t-c. The differences between shams and the lesion groups were more severe for Contracting trials. For Expanding trials, although the differences were in the predicted directions, they fell just short of significance (See Table 2). Recalling the discussion of the previous experiment, if it is true that the difference scores on Expanding trials represent a composite of two effects – modulation of running speed due to optic flow variables and at times 'hesitation' produced by detection of target movement, then one would predict that effects on contracting trials would be a somewhat more sensitive indicator of loss of the ability to analyze optic flow. This is because if detected as object motion, the Expanding targets could be construed as "looming" toward the animal and causing hesitation to a greater extent than could a target that was receding into the distance. The somewhat more consistent effect of posterior cortical lesions on performance on contracting trials is in accord with the argument from Experiment 2 that t-t-c analysis is cortically dependent.

We found no evidence for any differences in the performance of the V1 and Lateral animals on the runway task. Although it is possible that our VI lesions produced subtle collateral damage to lateral extrastriate cortex, we think it is more likely that the cortical processing that contributes to processing optic flow information requires cooperativity of VI and lateral areas. Anatomically, although it is possible for visual information to arrive at lateral extrastriate cortex independently of VI, it is clearly recognized that there are reciprocal connections between these areas (Benevento & Ebner, 1971; Cudmore, 1995; Montero, 1993; Olavarria & Montero, 1981; Sanderson, Dreher & Gayer, 1991; Spatz et al., 1991), and it is possible that effects of lesions in either area will also affect neurons in the other corresponding area.

EXPERIMENT 4

In Experiment 1 it was found that animals used t-t-c information from the target to modulate their deceleration, and may have also detected object motion in some of the trials. In Experiment 2, animals with visual cortex lesions lost their ability to use t-t-c information while animals with frontal lesions continued to modulate their locomotion to some extent, but were different from sham animals. In order to understand the difference between the response of sham animals and frontal animals, and to see if frontal and extrastriate areas are involved in detecting object motion, Experiment 4 was conducted with a variation of the stimuli used in Experiments 1 to 3.

1. Self motion and object motion

In the runway set up the change in size of the target was designed to mimic the target as being either 10 cm in front of or behind the actual target. The idea was to mislead the animal into believing that the change in size of the target was due to its self-movement. However, it is possible that the animals were detecting the change as being caused by object movement in some of the trials. Then the velocity profiles of the animals would reflect modulation because of self-motion cues obtained from t-t-c, and at times because of an awareness that the target was moving.

When an animal moves through the environment it needs to detect the presence of other animals moving around it (prey, predators, competitors), as well as gauge its own self-movement (to determine position, avoid collision, to guide heading, etc.). It makes intuitive sense that detection of object motion in the environment would be as important as being able to use self motion cues to guide actions. Motion information is useful when one can differentiate between changes in the visual image caused by moving objects, and those caused by one's own body, head, and eye movements.

2. Physiological evidence

Frost and Wylie (2000) have pointed out that object motion is detected through local motion and not global motion, whereas self- motion information derived from the optic flow depends on large areas of visual space. From their work on the pigeon visual system, Frost and Wylie (2000) show evidence that indicates that the accessory optic system is the neural substrate for the analysis of optic flow information. The neurons in this area have very large receptive fields, and continue to be activated by repeated stimulation from the flow field. Local object-motion-detecting neurons found in the tectofugal visual pathway (retina-optic tectum-nucleus rotundus-ectostriatum) are not activated by the optic flow stimuli.

Much of the primate work has focused on cortical areas. Results from the work of Duffy and Wurtz (reported in Duffy, 2000) in primates indicate three conclusions about the role of Medial Superior Temporal (MST) neurons: 1. MST neurons are sensitive to optic flow patterns that indicate heading of self-motion relative to the direction of gaze. 2. MST neurons are sensitive to the speed of optic flow patterns that give information about the structure of the environmental layout. 3. MST neurons are affected by vestibular information regarding self-movement, such that some MST neurons may differentiate between optic flow changes due to self-motion and others will detect motion that are caused by the movement of objects in the environment.

Electrophysiological studies in monkeys by Hietanen and Perrett (1996a, b) show that the majority of neurons in the Superior temporal polysensory area (STPa) respond selectively to visual motion originating from movements of external objects over stimulus motion caused by the animal's self movement.

Thus, it seems that, although in pigeons there are separate subcortical pathways that process object motion and cues from self-motion, in primates the extrastriate regions are involved in processing object motion and self-motion cues. Whether any such differentiation occurs in the rodent brain is currently unknown, because little work addressing this question has been done in rodent species. Experiment 4 thus attempts to address the involvement of frontal cortical and extrastriate regions in pathways that process such visual motion.

3. Frontal connections

To try to account for the effects that were seen in Experiment 2 it is necessary to look at the frontal subcortical and cortical connections to visual processing areas, to see whether the frontal region is part of a pathway that is involved with detection of object motion.

To identify the frontal regions' cortical and subcortical connections, one has to rely on the rat literature, as no literature on gerbil connections is currently available. Several frontal cortical areas can be documented on the basis of their receiving connections from nucleus medialis dorsalis of the thalamus (Krettek & Price, 1977; van Eden & Uylings, 1985). The frontal areas also receive thalamic afferents from medial anterior nucleus, the ventral nucleus, and the lateral posterior nucleus (LP) (Divac, Björklund, Lindvall, & Passingham, 1978) in addition to several other subcortical sites. The lateral posterior nucleus projects to a wide region of neocortex, including the occipital cortex and the posterior parietal cortex (PPC). These connections between the thalamic nuclei and cortical areas are similar to those found in primates, and may constitute a network of connections that play a role in the analysis of visuospatial information (Goldman-Rakic, 1987). In the monkey, the pulvinar projections to the PPC and prefrontal cortex are separate from those connecting with visual cortex, and, although similar work has not been done on rodents, it is possible that in the rodent brain too, there are similar discrete connections (Kolb, 1990a). Corticotectal connections have been described in the rat from the anteromedial cortex, an area that is considered homologous to the frontal eye field region in primates (Beckstead, 1979; Kolb, 1984; Leonard, 1969). Indirect connections have also been identified from the anteromedial cortex to the superior colliculus via the striatum and substantia nigra, pars reticulata (Somogyi, Bolam, & Smith, 1981).

The prefrontal cortex of rats is connected to the sensory regions and the posterior parietal region, with the connections from the visual areas to the prefrontal cortex being more extensive than somatosensory or auditory areas (Kolb, 1990b). In primates the dorsal and ventral pathways, which are said to modulate action and perception, respectively (Goodale & Milner, 1992), have connections to the prefrontal cortex. In the dorsal stream, connections from areas MST to posterior parietal cortex have shown to project to the dorsolateral prefrontal cortex, and in the ventral pathway connections through the inferotemporal area have been shown to project to the inferior convexity of the prefrontal cortex (Wilson, O'Scalaidhe, & Goldman-Rakic, 1993). Although no such connections have been clearly set down in gerbils, it is possible that frontal damage can extend to the extrastriate visual areas and cause difficulties in visual tasks.

It is clear that the frontal cortex in rodents is connected to other cortical areas and to common subcortical areas such as the striate and extrastriate cortex. So it is possible that damage to frontal areas may result in a loss of ability to process visual information efficiently.

As mentioned earlier in the introduction, whereas in primates the MT, MST and STPa areas have been shown to have specialized areas that either respond to object motion or self motion (Duffy, 2000; Hietanen & Perrett, 1996a, b), no empirical evidence has been reported on the neural substrates involved in separating object motion from self motion in rodents. Review of previous literature also does not tell us anything about the specific role that the frontal cortex plays in visual tasks in which object motion had to be differentiated from self-motion, so it is difficult to specify exactly how frontal cortex damage could cause a loss of object motion perception.

Experiment 4 was designed to probe the neural substrates that differentiate the perception of self-motion from object motion in the Mongolian gerbil. In order to separate object motion detection from the use of t-t-c, for this experiment, a new stimulus was introduced, in which a target either expanded or contracted very rapidly. It is unlikely that such rapid target size changes would be construed as being a consequence of self-motion. The sizes of the new stimuli were identical to those presented in earlier experiments, but the timing of change with respect to ongoing locomotion was manipulated. By using this design it was hoped that the role of the different areas in dissociating object- and self-motion would become clearer.

Based on findings from the previous three experiments, it was hypothesized that sham animals would use t-t-c information from the gradual trials to modulate their run. They would also show some reaction to the sudden changes in target size, and it was predicted that the effect would be larger for the Sudden expanding trials, because that would be construed as "looming" and get a stronger reaction from the animals. It was also predicted that frontal animals, although able to use t-t-c, would not be able to detect object motion in the Sudden trials, as they would be unable to dissociate motion caused by self-movement from that caused by object motion. Lastly, it was predicted that animals with lesions to lateral extrastriate cortex would be deficient in the use of t-t-c, as based on primate literature one would predict that animals with extrastriate lesions would be affected in the detection of object motion.

Method

Subjects

Twenty-two Mongolian gerbils served as subjects for this experiment. They were approximately 10 months at the beginning of training. All animal care procedures were the same as that for the previous experiments. The experiment was conducted in two parts to work with a reasonable number of animals at one time. The animals were trained, given the lesion (frontal, N=8), or lateral extrastriate, N=6)), or sham (N= 8) treatment, and tested for each part. The results from the two sets were combined to get data from twenty-two animals in all.

Apparatus

The same apparatus that was used in the three earlier experiments was used for this experiment.

Training

All the animals were trained to run to the end of the runway for a food reward in exactly the same manner as for the previous experiments.

Surgery

For the frontal treatment groups, the animals received large medial frontal lesions anterior to bregma and lateral to the midline, using the aspiration method. For the lateral group two small holes were drilled on each hemisphere, one 4 mm posterior to bregma and 6 mm lateral to the midline and the second 6 mm posterior to bregma and 6 mm lateral to the midline. Then radio frequency energy was used at these points to make small lateral extrastriate lesions. For the sham treatment, the animals received incisions; their skin was retracted and then sutured.

Testing

The protocol of testing the animals was different in this experiment as compared to the previous experiments. In the earlier experiments, the change in target size on expanding and contracting trials was yoked to the movement of the animal. For the present experiment this type of trial was called "gradual." Then a variation was introduced, wherein the target expanded or contracted very suddenly (within 50 to 60 ms), when the animal crossed the first sensor. This type of changing trial was called "sudden". For the sudden trials, the size of the target changed from 4 cm to 6.6 cm for expanding trials and from 3.5 cm to 1 cm for contracting trials. In order to produce sudden changes and gradual changes that produced exactly the same target size we had to change the range of target size changes in the original software to make it work. This change caused the target size change to be tripped much later (at about the 14th sensor), because up to that point the difference in size between a real and virtual target would be less than one pixel. We were cognizant of the fact that this change might dampen the effect of the use of t-t-c, as it would cause the virtual target to appear less-ahead of or less- behind- the earlier stipulated 10 cm.

Testing was done over 6 days. On each testing day the animals received either expanding or contracting trials, which included a gradual trial, a sudden trial, a matched static trial, and 17 normal trials. Thus, on days 1, 3, and 5, the animals received only expanding trials and for days, 2, 4, and 6 they received only contracting trials. All the test trials were conducted using a starting distance of 200 cm for this experiment. For the normal trials, in which different-sized static targets were used, the animals started the runs from various starting distances as in the earlier experiments.

Histology

The animals were perfused, their brains were extracted, and histology was done following the same procedures as that of Experiments 2 and 3.

Results

Anatomical results

The animals' brains were treated in exactly the same way as for the earlier experiments and reconstructed to verify the lesion sites, and to assess the extent of damage.

For the eight frontal animals, the damaged areas were largely in areas 4 and 6 in the frontal cortex. For most of the animals the lesions did not start right at the frontal pole, and some sparing of tissue was observed. In at least three of the animals the lesions extended more caudally, damaging the parietal cortex. Although no direct damage to subcortical structures from cuts was observed, the lesions of three of the animals were deep, damaging in addition to the frontal cortex, the corpus callosum, and the cingulate cortex (one animal). The lesions of 6 of the animals were medial, and restricted primarily to the motor cortex, whereas the lesions of two of the animals extended more laterally, damaging the somatosensory cortex. Examination of the ventromedial nucleus of the thalamus indicated clear cell loss and gliosis in all the animals, confirming the extent of cortical damage.

The radio-frequency lesions of the 6 lateral animals were small and focal and none of them extended beyond the cortex to deeper areas. Most of the animals had damage to areas 18a or 19, with the damage in one animal close to the primary visual cortex in one hemisphere. It was difficult to document subcortical damage to the lateral posterior nucleus and dorsal lateral geniculate nucleus of the thalamus, and that may be because the lesions were very small.

Behavioural Results

For this experiment we expected to see the effects of the sudden changes in target size to show early in the trajectory of an animal's run, and the effects of the use of t-t-c to be revealed during the deceleration phase closer to the target, so it was necessary to look at all 18 photobeam distances. For statistical analysis, the velocity profiles of the animals were divided into two phases, an early (sensors 1-9) phase and a late (sensors 10-18) phase, which were examined separately (See Figures 14, 15, & 16).

Early phase: A 4-way mixed ANOVA, with one between-group factor (Treatment: shams, frontal lesions, lateral extrastriate lesions), and 3 within-group factors (Probe: Expanding or Contracting trials, Trials: sudden, gradual or static, and Distance: the distance of the photobeams from the target along the runway), was conducted on the velocities recorded from photobeam sensors located between 90 and 50.25 cm from the target. Appendix E gives the ANOVA table for the early phase velocities. Table 3 shows the significant effects found for the early phase of the run of the animals.

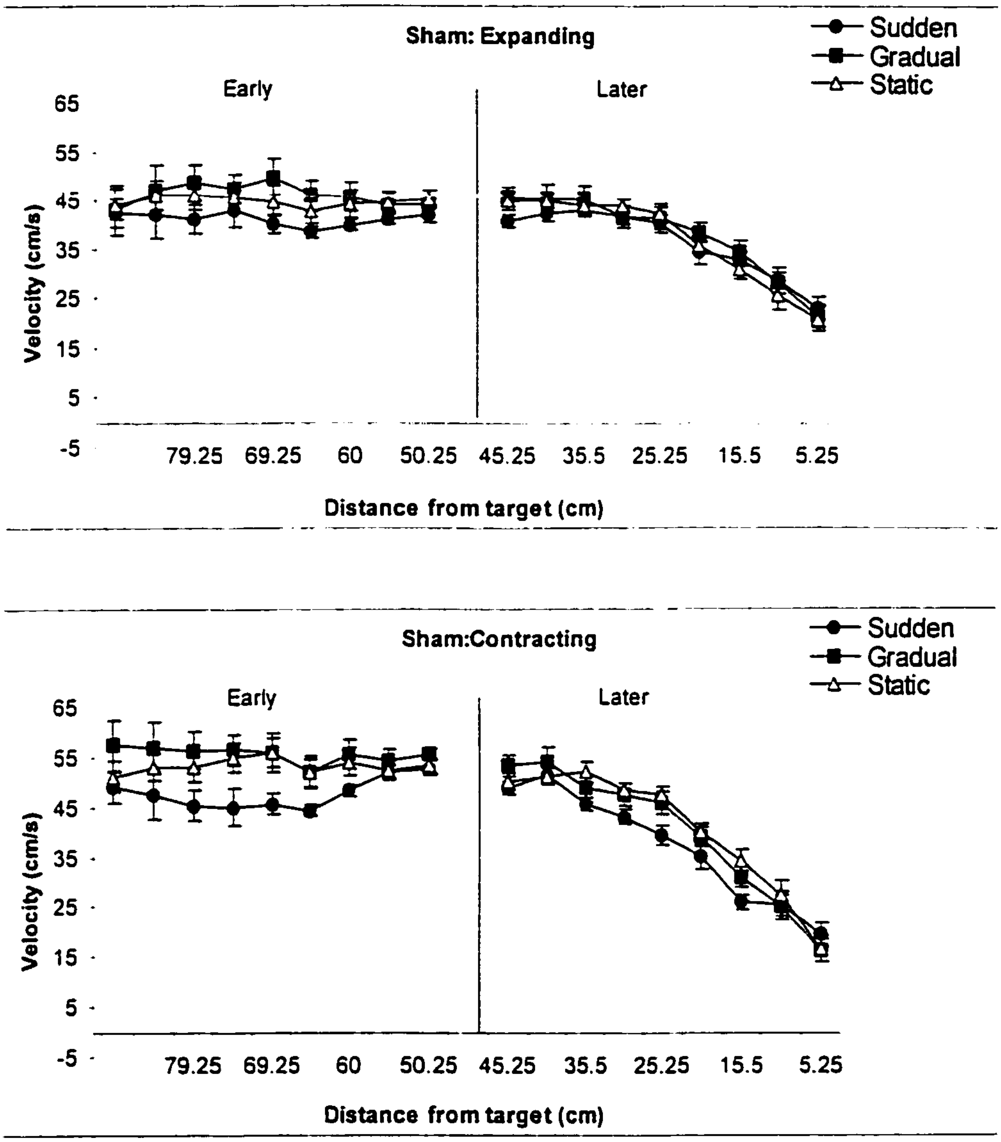


Figure 15: Velocity profiles for Sham animals for the three types of trials over the early and later phase. Separate graphs are shown for Expanding and Contracting probes. Error bars show standard error of means.

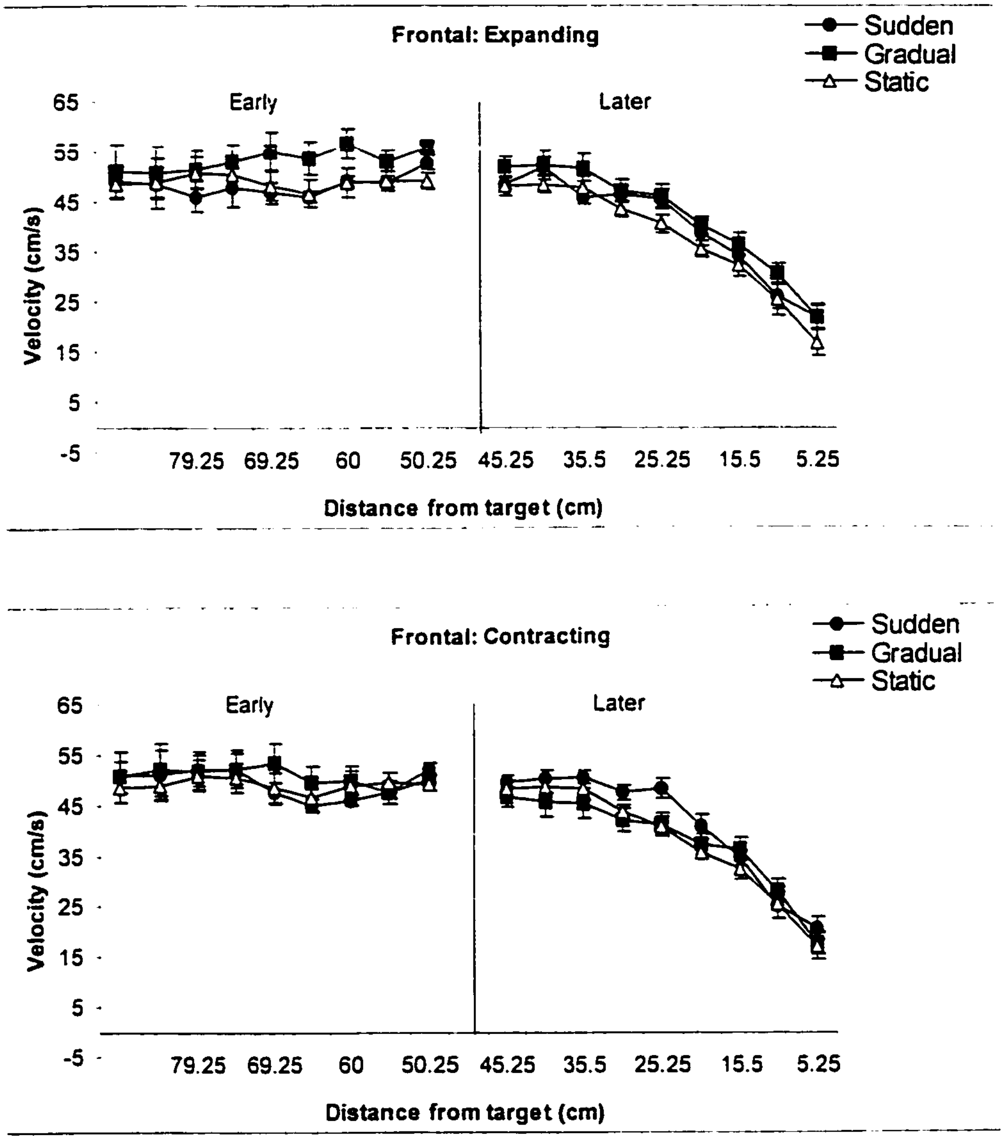


Figure 16: Velocity profiles for Frontal animals for the three types of trials over the early and later phase. Separate graphs are shown for Expanding and Contracting probes. Error bars show standard error of means.

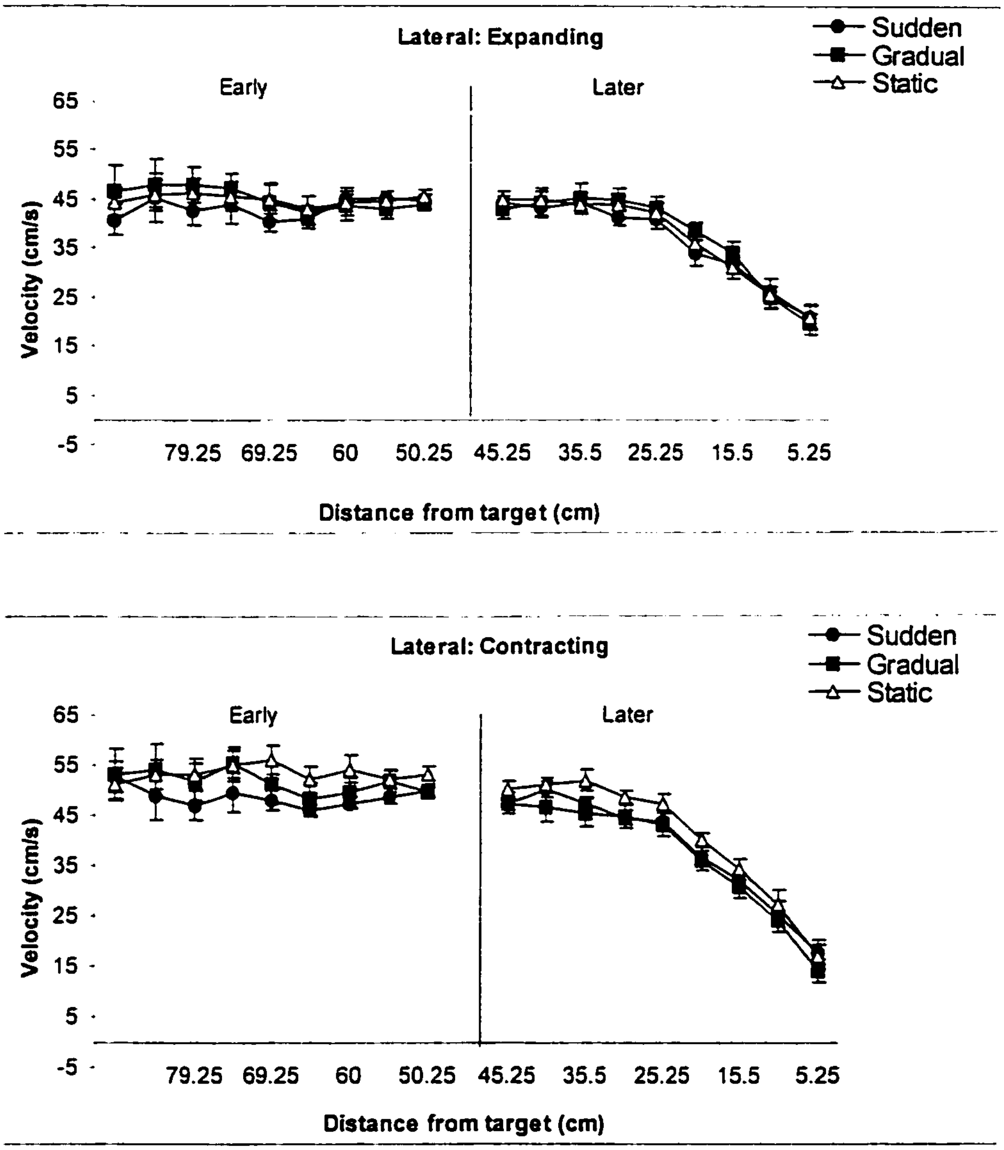


Figure 17: Velocity profiles for Lateral animals for the three types of trials over the early and later phase. Separate graphs are shown for Expanding and Contracting probes. Error bars show standard error of means.

Table 3: Significant results from the ANOVA for early phase of the run

Significant differences for velocity	**F values and p values**
Probe x Distance	$F_{(8, 152)} = 2.07$, $p = 0.042$
Trials x Distance	$F_{(16, 304)} = 1.90$, $p = 0.02$
Trials	$F_{(2, 38)} = 7.05$, $p = 0.002$
Distance	$F_{(8, 152)} = 3.56$, $p = 0.001$

Although differences were in the predicted direction and the main effect of treatment was found to be close to significance ($F_{(2, 19)} = 2.83$, $p = 0.083$) for the early phase of the runs, no treatment effects of interest were found to be significant [Trials x Treatment ($F_{(4, 38)} = 0.97$, $p = 0.434$); Probe x Trials x Treatment ($F_{(4, 38)} = 0.09$, $p = 0.985$)]. Because the design of this study was aimed at understanding effects of the lesions on the use of t-t-c and detection of object motion, the significant results obtained in Table 3 were probed.

Late phase: Similarly to the early phase, a 4-way mixed ANOVA, with one between-group factor (Treatment: shams, frontal lesions, lateral extrastriate lesions), and 3 within-group factors (Probe: Expanding or Contracting trials, Trials: sudden, gradual or static, and Distance: the distance of the photobeams from the target along the runway), was conducted on the velocities recorded from photobeam sensors located between 45.25 and 5.25 cm from the target. Table 4 shows the significant effects found for the later phase of the run of the animals.

Table 4: Significant results from the ANOVA for later phase of the run

Significant differences for velocity	F values and p values
Trials x Treatment	$F_{(4,38)} = 3.52$, $p = 0.015$*
Distance x Treatment	$F_{(16,152)} = 1.986$, $p = 0.017$ *
Distance	$F_{(8,152)} = 212.15$, $p < 0.001$*
Probes x Trials	$F_{(2,38)} = 2.975$, $p = 0.063$ +

The Trials x Treatment interaction was probed further to understand the treatment effects for running velocities for the three types of trial. Because the stimulus for Expanding and Contracting trials was different in terms of its motion and we expected the gerbils to behave differently for the two types of probes, I decided to look at treatment effects over the different trials separately for Expanding and Contracting trials.

It was seen that for the later phase of Expanding trials there was only a main effect of distance ($F_{(8,152)} = 145.6$, $p < 0.001$), which as mentioned earlier, is to be expected when the runway is of a particular length and the animals have to stop at the end. It was seen that the treatment interaction effects found in the main ANOVA were largely because of the later phase of the Contracting trials. A Trials x Treatment interaction was almost significant ($F_{(4,38)} = 2.51$, $p = 0.058$), and a Distance x Treatment interaction ($F_{(16,152)} = 2.67$, $p = 0.001$) and a main effect of Distance ($F_{(8,152)} = 166.39$, $p < 0.001$) were found to be significant.

Note: *- significant; + - close to significance

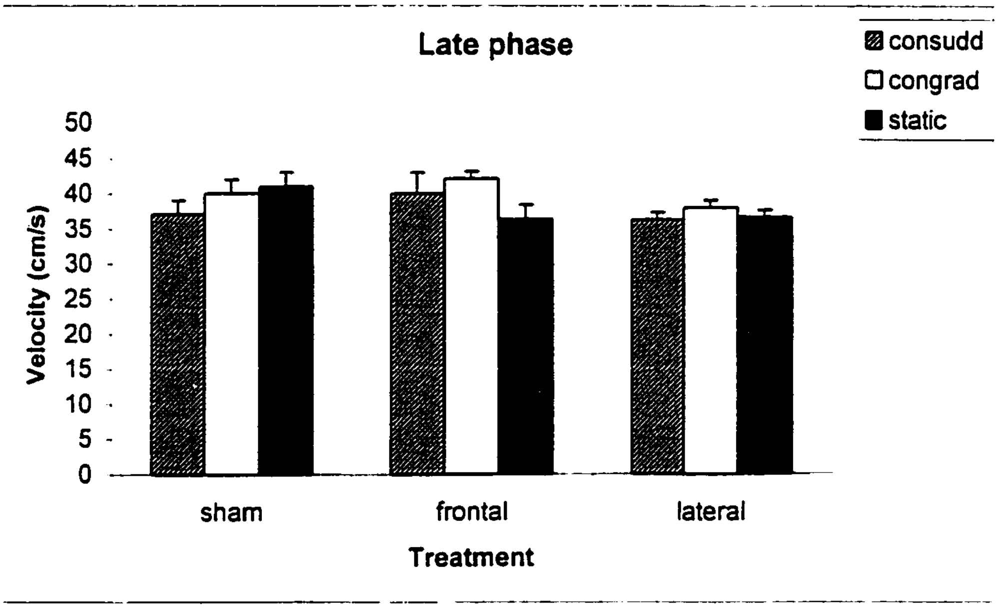


Figure 18: Trial x Treatment interaction for the later phase of Contracting probes. Values are Means + standard error of means.

Figure 18 shows the Treatment x Trials interaction and Table 5 indicates the trials differences of the animals, within each treatment.

Table 5: Results for the Treatment x Trial analysis for the later phase of the Contracting trials.

Treatment	**Trials** (Mean & SD)	**Comparisons**	**t - scores and significance**
Sham	Sudden M= 0.3714, SD=0.06 Gradual M= 0.4009; SD=0.08 Static M= 0.4107; SD=0.02	Sudden vs. Gradual Sudden vs. Static Gradual vs. Static	t(7) = -1.14, p =.293 ns t(7) = -2.29, p =.056 + t(7) = -0.40, p =.698 ns
Frontal	Sudden M= 0.4009, SD=0.04 Gradual M= 0.4223; SD=0.04 Static M= 0.3651; SD=0.03	Sudden vs. Gradual Sudden vs. Static Gradual vs. Static	t(7) = -1.34, p =.221 ns t(7) = 2.27, p =.057 + t(7) = 3.78, p = .007*
Lateral	Sudden M= 0.3637, SD=0.04 Gradual M= 0.3807; SD=0.04 Static M= 0.3676; SD=0.03	Sudden vs. Gradual Sudden vs. Static Gradual vs. Static	t(5) = -.82, p =.448 ns t(5) = -.46, p =.665 ns t(5) = 0.60, p =.576 ns

Even though the velocity profiles of sham animal and laterals were mostly in the predicted direction (Figures 14 and 16), significant trial differences were found only for the later phase of the Contracting trials.

Note: *-significant; ns- non-significant; +- close to significance

The velocity profiles of the frontal animals were different from those of the shams and laterals (Figure 16).

As seen in Table 5, for the later phase of the contracting trials, for sham animals the difference between sudden and static trials was close to significance, and no other differences were significant. Shams have shown no effects of the use of t-t-c in this phase. For frontal lesioned animals, the difference between gradual and static trials was significant, while that between sudden and static was close to significance. However, it must be noted that the differences between sudden and static trials, and gradual and static trials for frontal lesioned animals is because the animals have run very slowly for static trials. Thus, while the differences between sudden and static trials for shams is due to the animals slowing down for sudden trials, those for frontal lesioned animals is because of the animals running faster for sudden trials, or running slower for static trials. No trial differences were significant for the lateral lesioned animals, and the animals seem unable to use information from the target to modulate their runs. The effect of the gradual trials is dampened in this experiment on the whole as compared to the previous experiments. In order to better understand the significant results, differences over the three types of trials for the three treatments were also assessed. Comparisons showed no significant differences between treatments for any of the different trial types.

One matter of concern in the present experiment is the difference between sham animals and lateral lesioned animals for static trials alone. We had seen in the past experiments that differences in the velocity profiles of the animals from the different treatment groups came largely from the probe trials. In this experiment significant treatment effects were seen for the static trials ($F_{(2,19)} = 4.30$, $p = 0.03$), and lateral animals ($M = 0.4103$;

SD=0.03) ran significantly slower than sham animals (M= 0.4705, SD=0.05) (t(19) = 2.88, p < .01).

Discussion

Although the results from this study did not completely support the predictions made about the detection of object motion, some trends in the predicted direction were seen. We had expected to see the effects of sudden trials in the early phase of the runs, but significant differences for shams and laterals in the predicted direction were found in the later phase, and that too only for Contracting trials.

For sham animals there was hesitation or slowing down for both sudden contracting as well as sudden expanding trials. Sudden movement of objects in an otherwise stationary environment, especially for expanding trials, should have produced avoidance behaviour as it would have been similar to looming. However, it is reasonable that any unexpected movement in the environment would get a reaction from the animal and prevent it from running rapidly toward the target.

The frontal lesioned animals showed effects for the gradual trials as can be expected from the use of t-t-c to some extent. The frontals slowed down for the sudden trials, as compared to the static trials, in the later phase of the contracting trials (as reported in the results section). However, over the entire velocity profile the frontals did not slow down for sudden trials, and surprisingly even ran faster for the later half of the Expanding trials. Given the limited information available about the role of the frontal cortex in such tasks it is difficult to speculate on what is being seen with frontal animals here.

While frontal lesioned animals showed some probe effects to the gradual trials, the effects for the sham animals was not evident. This lack of strong probe effects in shams is of concern, and may have been an effect of the software changes we had made to accommodate the sudden trials. As mentioned in the methods section, in order to match the end size of the sudden and gradual targets, software modifications had to be made. The result of this modification was that the change in target size took place over a smaller distance as compared to the previous experiments, and may have resulted in a dampening of the effect of Expanding and Contracting trials for the sham animals.

Another obvious effect that was not seen in the earlier experiments was the difference in the velocity profiles for the static runs between the sham and lateral lesioned animals. For some reason, in this experiment, lateral animals ran slower than shams for the static trials. Though not statistically significant the frontal animals also ran slower than the sham animals. This would indicate that the results from this experiment have to be taken with some caution, as the animals with lesions may have been experiencing some other difficulties that were not obvious behaviourally and from the anatomical examination. Lesions from Experiment 4 were very comparable to the lesions from Experiments 2 and 3, and were in no way more extensive than the earlier lesions.

The only factor that was conspicuously different in Experiment 4 as compared to the earlier three experiments was the testing protocol. Because there were only two probe trials and two matched static trials on any given day (as compared to four probes and four matched static trials in Experiments 1-3), they were embedded in a larger number of normal trials and were in fact less frequent per day for this experiment. Another difference in protocol was that for the earlier experiments the starting points for the probe and matched static trials varied among four distances, and for Experiment 4 in order to simplify the design only one starting distance was used. However, we believe that because all the normal trials were started from varying distances along the runway, having these two probe trials and the matched static trials start from a fixed distance of 200 cm should not have made a big difference, and can in no way account for the slow static trial runs of the lateral lesioned animals.

One probable reason for the differences observed in this experiment as compared to the earlier experiment could be the new stimulus that was introduced. In our earlier experiments and for the gradual trials in this experiment, the changes in target size were subtle and cleverly yoked to the animal's movement, so as to appear to be caused by self-motion. On the other hand the sudden target changes introduced here were meant to be very rapid, and be noticeably caused by object motion. This sudden motion and change in size could have destroyed the illusion of the white circle being construed as an object by the animals, and they may have ceased to use it as a reliable source of t-t-c. In their study of distance estimation, Ellard et al. (1984) had indicated that a number of sources might contribute unequally to the final computation of distance, and if one of these sources were unavailable for some reason an animal would rely more heavily on another.

On the whole in this experiment, on the basis of the Sudden and Gradual trials, the predictions made that shams would be able to detect the obvious object motion, and be able to use t-t-c for the gradual trials, whereas frontals would be impaired in detecting object motion (while still using t-t-c from the gradual trials) and that laterals would not be able to detect object motion and also be impaired in their use of t-t-c from the gradual trials, could not be verified with confidence.

GENERAL DISCUSSION

Animals need to be able to use rapidly available information to guide actions, and the ecological model (Gibson, 1950) and optical variable t-t-c (Lee, 1976,1980) provide an elegant possibility. It is likely that in the natural environment gerbils have to contend with unfamiliar terrain, where they need to estimate distance of, or modulate their actions according to, unfamiliar objects. In such cases it will be more economical for the gerbils to use dynamic information that is available from the immediate environment to control their actions.

The present study set out to understand the use of t-t-c, which is an optical variable that is part of the optic flow phenomenon. Because past studies in other species that have shown the use of t-t-c have been criticized for various reasons, ranging from lack of control in natural settings, to not using set-ups like those that occur in reality, we used rigorously controlled settings, and movement on the part of the animals, as well as the target to study the use of t-t-c. In order to clearly establish the use of t-t-c we restricted the target to a single solid circle, to obtain control over as many visual cues as possible. The studies reported in Experiments 1-3, indicate that animals use t-t-c information to modulate their locomotion. Although all attempts were made to control for other cues in the set-up, the fact that the modulation of running speed fell short of theoretical prediction suggests that gerbils are using other sources of information in combination with target size change to monitor target distance. An animal's use of visual information is likely to depend on the task requirements, and in the absence of other sources of reliable information from vision, such as retinal image size, depth perception, distance cues, etc., t-t-c is used to control deceleration.

Though vision plays a very important role in visually guided locomotion, other sources that include kinesthetic and vestibular information, or even echolocation information from the sounds of their footfalls in the runway might have guided an animal's run. This may account for the individual differences seen in the velocity profiles of animals in response to the stimulus. By varying starting distance and target size randomly, we made all attempts to remove cues that the animals could use to gauge how far they had to go. However, it is important to remember that these animals had received considerable training in the runway, and in spite of the varying start distances, could likely learn how to use other subtle sources of information to shape their velocity profiles. As well, the animals might have been facilitated in their deceleration by cues from the end of the runway from the small amount of luminance from the target, as well as luminance differences between the end of the runway and the computer screen.

It is possible that, in spite of our endeavour to make the target changes subtle and yoked to the animal's movement, the animals detected the change as being caused by object motion for some trials. This would have caused a hesitation, as focusing on sudden changes in the environment is evolutionarily important to any animal. Visual motion is useful when an animal can differentiate between motion caused by one's own movement and that arising from objects in the environment, but it is possible that in a situation wherein other visual cues have been deliberately removed, and the available cue is manipulated, it can cause some errors in its use.

In the past, work with non-primates has designated the subcortex as being the area where t-t-c is processed (Sun & Frost, 1998b; Wang & Frost, 1992; Wylie & Frost, 1990), whereas work in primates has pointed to extrastriate cortex as a region for processing t-t-c. In rodents, the cortex has been shown to modulate the function of subcortical areas in many visual tasks, and we have shown cortical involvement in the use of t-t-c for gerbils. Visual cortex lesions attenuated an animal's ability to use t-t-c information to effectively modulate its locomotion, whereas animals with frontal lesions were not affected as adversely. We also found that small focal lesions in the primary visual cortex and lateral extrastriate regions render an animal unable to use t-t-c efficiently to modulate its locomotion. Further investigation into the neural substrates underlying the use of t-t-c should examine the effect of focal lesions in other areas, like the temporal areas, the parietal area, and the cerebellum, which have connections with the visual areas and are deemed to have motion-processing neurons.

Experiment 4 was different from the first three experiments, as it was designed to separate processing of self-motion that is used to judge t-t-c from object-motion processing that gives cues about the environment. Although no clear evidence was obtained from this study to support the notion that the frontal area is involved in object motion perception, or that the lateral extrastriate region is not, some trends were noticeable. It is possible that our sudden targets did not quite achieve what they were intended to, but it is interesting to see that in the later half for Contracting trials, differences between sudden and static targets were almost significant for shams.

Results from the present study show clearly that animals do not rely only on t-t-c information to modulate their locomotion. As such, Gibson's ecological model and its derivatives do not tell the whole story. Animals can pick up optical variables and use them as important sources of information to control their action. In the natural environment, where animals may come across unfamiliar stimuli, it is likely that readily available information that does not rely on memory or computations will be used. However, it seems necessary that animals have to rely on computation of factors like distance, size etc, for fine-tuning and precision of the use of visual information. Animals need a variety of resources to move about in a complex environment, and it is necessary for efficiency and survival that they have the capability of accessing and using as many options as possible. It is very likely that the ecological approach and the computational approach are complementary, with the ecological approach operating at a more global level of analysis.

Limitations of this study

The detection of t-t-c, although a reliable method for avoiding potentially harmful collisions in the environment, can only solve a small subset of problems in navigational control. In order to negotiate the cluttered environment successfully, animals must process the complex patterns of visual motion that are produced by the various visual surfaces in the form of optic flow. Hence it is desirable that in order to investigate the use of these more complex optic flow patterns in gerbils, the apparatus needs to be modified to present wide-field stimuli that can be animated so as to produce misleading optic flow just as the expanding and contracting single targets produced misleading t-t-c information in this study.

Some of the most compelling evidence for dissociation of visual functions in human beings has come from the analysis of pattern deficits in patients with damage to specific areas of the brain. In animals, the lesion method gives convincing evidence for the involvement of particular areas in the use of a studied behaviour, but it is important to keep in mind some of the limitations of the lesion technique. The lesion method removes an area and then determines what function has been lost. This method does not reveal whether the function was lost because it depended precisely on that area that was removed, or whether it depended on an area connected to the removed area. It is important that evidence uncovered by the lesion technique is supplemented with anatomical and physiological studies.

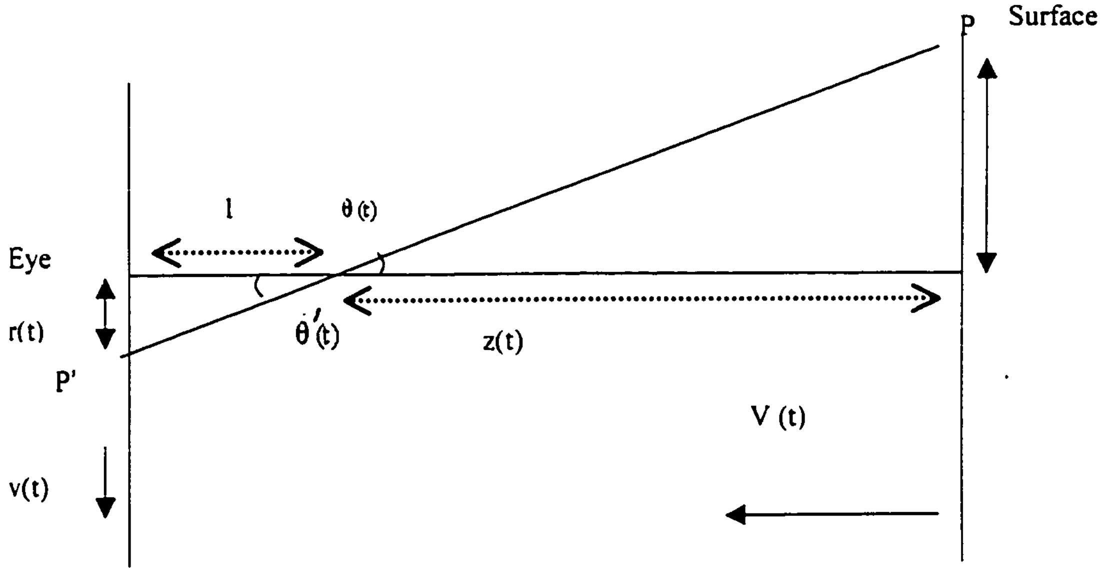
SUMMARY

In summarizing the main findings of the present investigation it was seen that animals use t-t-c to modulate visually guided locomotion. It is clear that t-t-c is not the only source of information, and that animals rely on other sources of information as can be seen by the individual differences. There is cortical involvement for the use of t-t-c in gerbils, and the damage to the visual cortex, as well as small lesions to primary visual cortex and lateral extrastriate regions can cause attenuation of the use of t-t-c. This indicates that in gerbils, either the whole of the visual cortex or different areas in the visual cortex, because of their connectivity are involved in t-t-c processing. Frontal cortical lesions do not cause complete loss of the ability to use information from t-t-c, but animals with frontal damage behave differently from sham animals. From the results of this study, it can be seen that frontal regions are not involved in the use of t-t-c, but may be involved in other aspects of using information from the stimulus (like detecting the motion of the stimulus) and thus affect behaviour in that respect.

Appendix A

Estimation of time-to-collision

(Adapted from Lee (1976)



Schematic representation of an animal's eye approaching a surface with velocity V (t).

At time (t) the surface is distance z (t) away from the nodal point of the lens.

A texture element in the optic flow (P) has an image P' projected on the retina.

At time t, P' is a distance r (t) from the center of the expanding optic flow field, and expanding with velocity v (t).

The ratio of the distance of a point from the centre of expansion to its velocity away from the center (r(t)/v(t)) specifies tau.

Tau can also be specified by the ratio of the solid angle subtended at the eye by an object moving towards an observer to the rate of change of this angle (θ (t)/θ'(t))

Appendix B

Experiment 1: ANOVA (repeated measures) table for Velocity difference scores

Tests of Within-Subjects Effects

Measure: MEASURE_1

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
PROBE	1.035	1	1.035	17.8	.002
Error(PROBE)	.523	9	5.807E-02		
START	.129	3	4.292E-02	1.364	.275
Error(START)	.849	27	3.146E-02		
DISTANCE	5.375E-02	8	6.719E-03	1.112	.366
Error(DISTANCE)	.435	72	6.045E-03		
PROBE * START	3.410E-02	3	1.137E-02	.302	.824
Error(PROBE*START)	1.017	27	3.767E-02		
PROBE * DISTANCE	6.282E-02	8	7.852E-03	2.059	.051
Error(PROBE*DISTANCE)	.275	72	3.813E-03		
START * DISTANCE	8.075E-02	24	3.365E-03	.818	.711
Error(START*DISTANCE)	.888	216	4.111E-03		
PROBE * START * DISTANCE	7.776E-02	24	3.240E-03	.692	.857
Error(PROBE*START*DISTANCE)	1.011	216	4.682E-03		

Tests of Between-Subjects Effects

Measure: MEASURE_1

Transformed Variable: Average

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
Intercept	9.475E-02	1	9.475E-02	2.033	.188
Error	.419	9	4.660E-02		

Appendix C

Experiment 2: ANOVA table for Velocity difference scores

Tests of Within-Subjects Effects

Measure: MEASURE_1

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
PROBE	.661	1	.661	13.808	.002
PROBE * TREATMENT	.237	2	.118	2.473	.114
Error(PROBE)	.814	17	4.788E-02		
START	7.966E-02	3	2.655E-02	2.139	.107
START * TREATMENT	7.045E-02	6	1.174E-02	.946	.471
Error(START)	.633	51	1.241E-02		
DISTANCE	6.705E-02	8	8.382E-03	3.429	.001
DISTANCE * TREATMENT	3.439E-02	16	2.149E-03	.879	.594
Error(DISTANCE)	.332	136	2.444E-03		
PROBE * START	.126	3	4.201E-02	1.741	.170
PROBE * START * TREATMEN	.320	6	5.331E-02	2.209	.057
Error(PROBE*START)	1.231	51	2.414E-02		
PROBE * DISTANCE	3.274E-02	8	4.092E-03	1.415	.195
PROBE * DISTANCE * TREATMEN	.120	16	7.485E-03	2.589	.002
Error(PROBE*DISTANCE)	.393	136	2.891E-03		
START * DISTANCE	6.637E-02	24	2.766E-03	1.201	.236
START * DISTANCE * TREATMEN	8.708E-02	48	1.814E-03	.788	.845
Error(START*DISTANCE)	.940	408	2.303E-03		
PROBE * START * DISTANCE	5.631E-02	24	2.346E-03	.773	.772
PROBE * START * DISTANCE *	.108	48	2.257E-03	.743	.897
Error(PROBE*START*DISTANCE)	1.239	408	3.036E-03		

Tests of Between-Subjects Effects

Measure: MEASURE_1
Transformed Variable: Average

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
Intercept	4.272E-02	1	4.272E-02	2.552	.129
TREATMENT	6.464E-02	2	3.232E-02	1.931	.176
Error	.285	17	1.674E-02		

Appendix D

Experiment 3: ANOVA table for Velocity difference scores

Tests of Within-Subjects Effects

Measure: MEASURE_1

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
PROBE	.167	1	.167	13.416	.003
PROBE * TREATMENT	.284	2	.142	11.431	.001
Error(PROBE)	.174	14	1.244E-02		
START	.337	3	.112	13.868	.000
START * TREATMENT	3.472E-02	6	5.787E-03	.714	.640
Error(START)	.340	42	8.107E-03		
DISTANCE	3.923E-02	.340	14.000	2.E-02	.001
DISTANCE * TREATMENT	1.135E-02	16	7.097E-04	.507	.939
Error(DISTANCE)	.157	112	1.399E-03		
PROBE * START	2.994E-02	3	9.981E-03	1.202	.321
PROBE * START * TREATMENT	5.155E-02	6	8.591E-03	1.035	.417
Error(PROBE*START)	.349	42	8.303E-03		
PROBE * DISTANCE	9.448E-03	8	1.181E-03	.953	.477
PROBE * DISTANCE *	1.658E-02	16	1.036E-03	.836	.643
Error(PROBE*DISTANCE)	.139	112	1.240E-03		
START * DISTANCE	4.089E-02	24	1.704E-03	1.351	.128
START * DISTANCE *	8.293E-02	48	1.728E-03	1.370	.060
Error(START*DISTANCE)	.424	336	1.261E-03		
PROBE * START * DISTANCE	3.811E-02	24	1.588E-03	1.325	.143
PROBE * START * DISTANCE *	5.026E-02	48	1.047E-03	.874	.709
Error(PROBE*START*DISTANCE)	.403	336	1.198E-03		

Tests of Between-Subjects Effects

Measure: MEASURE_1

Transformed Variable: Average

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
Intercept	8.197E-02	1	8.197E-02	4.163	.061
TREATMENT	1.471E-02	2	7.353E-03	.373	.695
Error	.276	14	1.969E-02		

Appendix E

Experiment 4: ANOVA table for the early phase for Velocity.

Tests of Within-Subjects Effects

Measure: MEASURE_1

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
PROBE	1.085E-02	1	1.085E-02	.292	.595
PROBE * TREATMENT	1.991E-02	2	9.953E-03	.268	.768
Error(PROBE)	.706	19	3.717E-02		
TRIALS	.332	2	.166	7.046	.002
TRIALS * TREATMENT	9.147E-02	4	2.287E-02	.972	.434
Error(TRIALS)	.894	38	2.353E-02		
DISTANCE	9.737E-02	8	1.217E-02	3.556	.001
DISTANCE * TREATMENT	2.534E-02	16	1.584E-03	.463	.961
Error(DISTANCE)	.520	152	3.423E-03		
PROBE * TRIALS	7.123E-02	2	3.561E-02	1.417	.255
PROBE * TRIALS * TREATMENT	9.011E-03	4	2.253E-03	.090	.985
Error(PROBE*TRIALS)	.955	38	2.513E-02		
PROBE * DISTANCE	5.018E-02	8	6.273E-03	2.066	.042
PROBE * DISTANCE *	4.411E-02	16	2.757E-03	.908	.561
Error(PROBE*DISTANCE)	.461	152	3.036E-03		
TRIALS * DISTANCE	7.759E-02	16	4.849E-03	1.897	.020
TRIALS * DISTANCE *	7.270E-02	32	2.272E-03	.889	.644
Error(TRIALS*DISTANCE)	.777	304	2.556E-03		
PROBE * TRIALS * DISTANCE	9.604E-03	16	6.002E-04	.224	.999
PROBE * TRIALS * DISTANCE *	4.116E-02	32	1.286E-03	.479	.993
Error(PROBE*TRIALS*DISTANCE)	.816	304	2.685E-03		

Tests of Between-Subjects Effects

Measure: MEASURE_1

Transformed Variable: Average

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
Intercept	276.208	1	276.208	1448.236	.000
TREATMENT	1.079	2	.540	2.830	.084
Error	3.624	19	.191		

Appendix F

Experiment 4; ANOVA table for the later phase for Velocity.

Tests of Within-Subjects Effects

Measure: MEASURE_1

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
PROBES	5.419E-03	1	5.419E-03	.354	.559
PROBES * TREATMENT	4.392E-03	2	2.196E-03	.143	.867
Error(PROBES)	.291	19	1.531E-02		
TRIALS	7.571E-03	2	3.785E-03	.384	.684
TRIALS * TREATMENT	.139	4	3.469E-02	3.516	.015
Error(TRIALS)	.375	38	9.867E-03		
DISTANCE	11.174	8	1.397	212.186	.000
DISTANCE * TREATMENT	.209	16	1.307E-02	1.986	.017
Error(DISTANCE)	1.001	152	6.583E-03		
PROBES * TRIALS	7.818E-02	2	3.909E-02	2.975	.063
PROBES * TRIALS * TREATMENT	4.012E-02	4	1.003E-02	.763	.556
Error(PROBES*TRIALS)	.499	38	1.314E-02		
PROBES * DISTANCE	3.213E-02	8	4.016E-03	1.639	.118
PROBES * DISTANCE *	3.235E-02	16	2.022E-03	.825	.656
Error(PROBES*DISTANCE)	.373	152	2.451E-03		
TRIALS * DISTANCE	4.131E-02	16	2.582E-03	1.043	.411
TRIALS * DISTANCE * TREATMENT	8.661E-02	32	2.706E-03	1.093	.340
Error(TRIALS*DISTANCE)	.753	304	2.476E-03		
PROBES * TRIALS * DISTANCE	1.845E-02	16	1.153E-03	.682	.811
PROBES * TRIALS * DISTANCE *	3.773E-02	32	1.179E-03	.698	.891
Error(PROBES*TRIALS*DISTANCE)	.514	304	1.690E-03		

Tests of Between-Subjects Effects

Measure: MEASURE_1

Transformed Variable: Average

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
Intercept	172.785	1	172.785	2935.125	.000
TREATMENT	.104	2	5.216E-02	.886	.429
Error	1.118	19	5.887E-02		

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