

## How movement is guided

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**Abstract.** The development of a theory of prospective guidance of movement - *general tau theory* - is described. The theory deals with the purposive guidance of bodily movements, including internal movements, by means of the patterns of flow in sensory arrays and the patterns of flow of electrical energy within the nervous system. The central idea is that movement is guided by *tau-coupling action-gaps*. All purposive movement of the body, and within the body, requires guided closure of action-gaps. An action-gap, generally defined, is the changing gap between a current state and a goal state. Examples are the distance action-gap between the hand and an object when reaching, the optical action-gap between the images of the hand and object in the optic flow-field, the suction action-gap when a baby is drawing in milk, the pitch action-gap when a singer is sliding between notes. Tau of an action-gap is the first-order time-to-closure of the action-gap, i.e., the current size of the action-gap divided by its current rate of closure. Tau-coupling means keeping the taus of two action-gaps in constant ratio during a movement. Theoretical analyses and experiments are summarized that offer explanations, through the tau-coupling of action-gaps, of how the taus of action-gaps are sensed, how patterned electrical activity in the brain guides movement, how space is action-scaled, how actions are fitted into available spatio-temporal slots, how a driver controls braking and steering, how infants guide their movements, how athletes guide their movements, how musicians create expression by the way they guide their movements. Applications of the theory to the diagnosis and treatment of movement disorders are also discussed.

"Let us begin by noting that *information about* something means only *specificity to* something. Hence, when we say that information is conveyed by light, or by sound, odor, or mechanical energy, we do not mean that the source is literally conveyed as a copy or replica. The sound of a bell is not the bell and the odor of cheese is not cheese. Similarly the perspective projection of the faces of an object (by the reverberating flux of reflected light in a medium) is not the object itself. Nevertheless, in all these cases a property of the stimulus is univocally related to a property of the object by virtue of physical laws. This is what I mean by the conveying of environmental information."

J. J. Gibson 1966 p187

"Whatever forms of the motor activity of higher organisms we consider, from elementary movements to multiphasic industrial processes, writing, articulation, etc., analysis suggests no other guiding constant than the form and sense of the motor problem and the dominance of the required result of its solution, which determine from step to step, now the fixation and now the reconstruction of the course of the program as well as the realization of the sensory correction."

N. Bernstein 1967 p133

"It is interesting to contemplate an entangled bank, clothed with many plants of many kinds, with birds singing on the bushes, with various insects flitting about, and with worms crawling through the damp earth, and to reflect that these elaborately constructed forms, so different from each other, and dependent on each other in so complex a manner, have all been produced by laws acting around us."

C. Darwin 1859

## **1 Beginnings**

To get around in the world and interact with others, humans and other animals have to perceive where their actions are leading and modify their movements to suit their purpose. That is, they have to prospectively control their movements. This article is about how they do that. It is a brief history of tau theory, from its beginnings in two papers on visual control of locomotion (Lee 1974; Lee 1976) up to general tau theory, which attempts to encompass all perceptual systems and all movement. The tau idea

started to germinate in the late sixties during discussions on perception that I had with James Gibson at Cornell. As a sapling, tau was optically biased. It was preoccupied with light and took no heed of other stimulus energy fields such as sound. However, as it developed, it embraced other energy fields, revealed hidden aspects of prospective control of movement and grew into general tau theory.

At rock bottom were two questions: Why do animals have perceptual systems and why do they have motor systems? Even cells have a remarkable array of sensors that can detect changes in light, vibration, chemical concentration, gravitational force, and electromagnetic fields. They also have sophisticated means of moving themselves, using cilia and flagella. The straightforward answers to the questions are, of course, that animals need motor systems to move themselves around in order to perceive the environment, secure food, avoid predators, mate and so on; and they need perceptual systems to prospectively control all of these movements. Thus perception and movement are mutually dependent: perception requires movement and movement requires perception. The perceptual and motor systems must, therefore, be coupled together by information to form a composite action system. Consequently, two fundamental questions are: What form does the information take and how is the coupling enacted? General tau theory attempts to answer these questions.

## **2 Principles of animal movement**

From the seminal work of James Gibson (1950, 1966, 1979) and Nikolai Bernstein (1967) can be distilled the following general principles of animal movement:

1. *Movement requires prospective control.* Animals have limited forces available for making a movement, and so foresight is required to guide the movement. If drivers do not prospectively control braking they run the risk of running out of braking force and crashing.
2. *The perceptual information guiding movement must extrapolate the movement into the future and must be readily available.* Rapid on-line prospective guidance of movement would not be possible otherwise.
3. *Movement requires constant intrinsic-cum-perceptual guidance.* Intrinsic guidance is necessary because animals have to fashion movements to their purpose. Perceptual

guidance is necessary because movements are produced by muscular forces interacting with external forces such as gravity, friction and wind, which are not fully predictable. Thus movements cannot be precisely programmed in advance: they need to be perceptually guided to follow their planned course. When singing, the voice is guided by inner music, but it also needs to be guided by hearing to keep it in tune.

4. *Movement guidance must be simple and reliable.* Even animals with very small nervous systems, such as insects, move rapidly and reliably with a precision comparable to our own. Just watch bees flying from flower to flower, for instance.

5. *There are simple universal principles of movement guidance in animals.* I include this conjecture because it follows naturally from the preceding principles. If in early evolution a principle of action had been discovered that worked, it is unlikely to have been thrown away, though it might have been modified.

Thus, an adequate theory of movement must explain how movements are intrinsically-cum-perceptually prospectively guided. It must explain the form of the guiding perceptual information that enables prospective control of movement. And it must be biologically plausible. My goal over the past thirty years has been to develop such a theory. The domain of the theory (general tau theory) is different from those of other current theoretical approaches to understanding movement, which are not concerned with movement guidance but rather with explaining the dynamics of movement production in terms of solutions to optimization problems (e.g., Alexander 1997; Flash and Hogan 1985), or with developing mathematical models of the physico-neural structure of the muscles and joints (Bizzi et al 1992; Feldman and Levin 1995), of the abstract underlying dynamics of movement (Beek et al 1995; Kelso 1995; Schmidt and Turvey 1994) and of processes for coping with noise in the sensorimotor system (Kording and Wolpert 2004). These are all important problems but space does not allow me to discuss them here.

### **3 Tau of a action-gap**

In developing tau theory, I started, as had Gibson and Bernstein, with a practical question. In my case the question was: how do drivers visually control braking? At first blush it might seem that a driver has to perceptually monitor the changing size, velocity

and deceleration of the *action-gap* to the obstacle and then mentally apply on the fly Newton's equations of motion to work out how to adjust the pressure on the brake pedal. However, this seemed a highly implausible control procedure. Analysis of the braking task (Lee 1976) revealed a much simpler solution: rather than use multiple information about the size, velocity and deceleration of the action-gap, simply use the *tau* ( $\tau$ ) of the action-gap. Tau is a measure of how an action-gap is changing. It is the time-to-closure of the action-gap at the current rate of closure, or, equivalently, the first-order time-to-closure of the action-gap. Though tau is measurable in time units, the concept is not a purely temporal one. Tau is a blend of space and time. It is perhaps the kind of quantity that Minkowski (1908) had in mind in his famous address inspired by relativity theory: "Henceforth space by itself, and time by itself, are doomed to fade away into mere shadows, and only a kind of union of the two will preserve an independent reality." The concepts of tau and action-gap are central to general tau theory and are discussed in the following sections<sup>1</sup>.

### 3.1 *Action-gap*

An action-gap is defined, in general, to be the changing gap between two measurable states. For example, the changing gap between the measurable state an animal is currently in and the goal state that it wants to be in is an action-gap. All purposeful actions entail controlling the closure of action-gaps, often in tandem. For instance, stepping forward to pick a fruit from a tree requires controlling the closure of the

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<sup>1</sup> The concepts of action-gap and tau defined here were formulated when developing general tau theory (Lee 1998). Tau was first formulated in a more restricted sense as an optic variable that specifies time-to-collision if the closing velocity is maintained (Lee 1976). The idea was broadened by introducing the concept of the tau-margin, defined as the time to nearest approach of an object to the point of observation (Lee, Young 1985). It was then further generalized as the tau function (in the mathematical sense) of a variable  $x$ , defined as  $\tau(x) = x/\dot{x}$ , where the dot signifies the first time derivative (Lee et al 1992). The tau of an action-gap  $x$  equals the tau function of  $x$ ,  $\tau(x)$ .

*angular* action-gap between the current gaze direction and the direction of the fruit in order to adequately visually control the reach; the *force* action-gap between the current force exerted through the foot on the ground and the force required to satisfactorily step forward; and the *distance* action-gap between the hand and the fruit in order to grasp the fruit. Singing also involves closing action-gaps, e.g., a *pitch* action-gap between the pitch of the voice and the destination pitch when sliding between notes, or an *energy* action-gap between the energy of the sound and the destination energy when singing a crescendo. Note that the physical dimension of the action-gap is different in all these cases, namely angle, force, distance, pitch, energy. Thus the concept of action-gap is not restricted to a particular physical dimension.

Controlling the closure of an action-gap requires perceptual information about the gap and how it is closing. Since action-gaps come in different physical dimensions, does this mean that the perceptual information about the gaps has to come in different physical dimensions too? It would lead to a complicated system of mixed-dimensions control. Maybe evolution has found a neater solution (it usually does) and animals sense all action-gaps in the same physical dimension. It is unlikely to be one of the dimensions we have considered so far (angle, force or distance) because that would give one type of action-gap (distance, say) a privileged position and so would not be a symmetrical solution. More likely, evolution has picked on the dimension that underlies the process of change of any action-gap, namely time. This is where the concept of tau comes in.

### 3.2 *Tau*<sup>1</sup>

The tau of an action-gap is the first-order time-to-closure of the action-gap, i.e., the time-to-closure of the action-gap at the current rate of closure<sup>2</sup>. (Note that tau is *not* in general the actual time-to-closure of an action-gap, because the velocity of closure of an action-gap may not be constant.) Tau of an action-gap is numerically equal to the ratio of the current size,  $x$ , of the action-gap to its current rate of closure,  $\dot{x}$ ; i.e.,  $\tau(x) =$

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<sup>2</sup> If the action-gap is expanding then tau is positive and is the first-order time-*from*-closure.

$x/\dot{x}$ . However, that does not imply that sensing tau requires sensing the size of the action-gap and its rate of closure. By analogy, though linear acceleration is numerically equal to the second time derivative of distance, it is sensed directly, without sensing distance or time, by the vestibular system that exploits Newton's third law of motion. Likewise tau could be sensed directly by virtue of physical laws (section(10)).

#### 4 Tau-dot and control of deceleration

Since tau extrapolates how an action-gap is changing, it affords information for prospectively controlling the action-gap. Analysis of the equations of motion of a decelerating action-gap reveal that the only information a driver needs to prospectively control on-going braking is *tau-dot* of the action-gap to the obstacle - i.e.,  $\dot{\tau}(\text{action-gap})$ , the temporal rate of change of  $\tau(\text{action-gap})$  (Lee 1976). If tau-dot of the action-gap is less than or equal to a half then the current deceleration, if maintained, is adequate to stop before the obstacle. If tau-dot of the action-gap is greater than a half then collision will ensue if the deceleration is maintained. Moreover, if the deceleration is adjusted so that

$$\dot{\tau}(\text{action-gap}) = k \quad (1)$$

where k is constant during the deceleration, then if  $k \leq 0.5$ , the action-gap will reach closure at zero velocity and so the vehicle will stop right at the obstacle, and if  $k > 0.5$ , the action-gap will reach closure at non-zero velocity and so collision will result.

(Figure 1 about here)

Humans and animals have been observed to keep  $\dot{\tau}$  constant to control their deceleration to a goal<sup>3</sup>. The following are some examples, using vision and hearing<sup>4</sup>

#### 4.1 Visually guided movements

Figure 1a illustrates stopping a vehicle right behind a stationary vehicle. The action-gap (m-g) is between the front of the moving vehicle and the back of the stationary one. Studies of drivers braking to a designated point on a test track and in a simulator (Lee 1976; Yilmaz and Warren 1995) indicated that they kept  $\dot{\tau}$  of the action-gap equal to a constant,  $k$  (equation 1). The mean  $k$  values were 0.42 and 0.51 respectively, which accord with the drivers stopping at the point.

Figure 1b shows a hummingbird (*Colibri coruscans*) docking on a feeder tube (Lee et al 1991a). During deceleration the bird kept  $\dot{\tau}$  of the action-gap between the tip of the bill and the entrance to the feeder tube equal to a constant,  $k$ . The mean  $k$  value was greater than 0.5, namely 0.71, meaning that the bill was still moving forward slightly as it reached the tube entrance. Thus the bird completed its deceleration after entering the tube. That way it obtained the food, which was at the base of the tube.

Figure 1c shows a pigeon landing on a perch (Lee et al 1993). During the landing deceleration the bird kept  $\dot{\tau}$  of the action-gap between its feet and the perch equal to a constant,  $k$ . The mean  $k$  value was 0.77, again greater than 0.5, meaning that the feet were still moving forward slightly as they contacted the perch. The last stage of stopping was achieved through contact with the perch. That way the bird avoided goofing by stopping short of the perch.

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<sup>3</sup> The ' $\dot{\tau}(\text{action-gap}) = k$ ' hypothesis is tested by linearly regressing  $\tau(\text{action-gap})$  on time. The hypothesis is generally considered to be supported if  $r^2 > 0.95$ , meaning that over 95% of the variance in the data is accounted for by the hypothesis. The regression slope is then taken as the measure of  $k$ .

<sup>4</sup> The somersaulting and bat studies were conceived later than the others, following the development of general tau theory.

Figure 1d shows a gymnast performing a forward somersault on a trampoline (Lee et al 1991b). She has to decelerate her angular velocity by extending her body to land upright on the trampoline. Here the action-gap (m-g) is an *angular* one, between her trunk and the vertical (figure 1d). Movement analysis of two gymnasts indicated they kept tau-dot of the action-gap equal to  $k$ , with a mean  $k$  value of 0.61. Since this is greater than 0.5 it means that the gymnasts landed while still rotating slightly. Their terminal angular velocity was dissipated through contact with the trampoline.

#### 4.2 Sonically guided movements

Figure 1e shows a bat (*Macroderma gigas*) using echolocation to slow down to pass, wings aslant, through a small aperture (Lee et al 1992). During deceleration the bat kept tau-dot of the action-gap between its head and the aperture equal to a constant,  $k$ . The mean  $k$  value was 0.79, again greater than 0.5, meaning that the bat reached the aperture still moving forward slightly and so flew smoothly through it.

Figure 1f shows a different echolocating bat (*Eptesicus fuscus*) flying in to land on a perch (Lee et al 1995). During the decelerative approach the bat kept tau-dot of the action-gap between its head and the perch equal to a constant,  $k$ . The mean  $k$  value was 0.70, meaning that the bat was still moving forward slightly as it reached the perch, the terminal braking being achieved at contact.

### 5 Initiating actions

Several studies indicate that tau of the action-gap between an effector and an object or surface can govern the timing of the initiation of a movement (e.g. Kaiser, Mowafy 1993; Lee, Reddish, 1981; van der Meer et al 1994), or of neural activity (Wang, Frost 1992), or discrimination of time of arrival (Regan, Hamstra 1993). However, in general what determines the timing of the initiation of actions is a complicated question because it depends on a number of factors. This makes doing research on the subject difficult. One problem is that it is frequently not critical when a movement should start, just providing it does not start too late. Thus individuals may differ in when they start

an action, depending e.g., on how cautious they are. Another problem is that the appropriate time, or range of times, to start an action generally depends on both the individual's skill and the environmental conditions. For example, when to start braking to stop safely at an obstacle depends on the driver's skill and knowledge of the vehicle's braking potential, as well as accurate perception of the condition of the road surface. Tau of the action-gap to the obstacle could be involved in such a task, but it is not the only information needed for safe braking. Drivers need to bring along to the task information picked up during previous experience. How a person acquires and uses such information needs to be researched.

Figure 2 about here

## **6 Fitting actions into spatio-temporal slots**

Timing the start of an action is but part of the more general problem of fitting actions into spatio-temporal slots. Moving through the environment is a four dimensional jigsaw puzzle. Actions have to fit both spatial and temporal constraints. Figure 2a shows a diving gannet (*Sula bassana*) streamlining its wings in preparation for entering the water. If it starts streamlining too late it will break its wings, too early it will lose steering power. It has to fit the streamlining action into a tight spatio-temporal slot as it plunges under gravity toward the water. A film analysis of the diving birds (Lee and Reddish 1981) indicated that they used the tau of the action-gap to the water to time the initiation of streamlining, rather than their height above the water or the actual time to contact (which was shorter than tau because they were accelerating under gravity). Presumably through experience the gannet acquires information about the tau of the action-gap to the water that will allow it sufficient time to streamline its wings.

An attempt was made to replicate the gannet study with human divers, but no volunteers could be found! Therefore an upside-down version of the experiment was run, as illustrated in figure 2b (Lee et al 1983). A football was dropped vertically down from different heights to a participant who leapt and punched it back up. The leaping-and-punching action had to fit into a precise spatio-temporal slot as the ball dropped

towards the participant and the participant leapt to meet it. Movement analysis indicated that they geared the flexion/extension of their punching arm and thrusting leg to the changing value of tau of the action-gap of the ball to the punching place, rather than to the ball's actual time to arrival at the place.

Figure 2c shows a ski-jumper performing the jump action (thrusting themselves from a crouch to upright) during their final approach to the lip of the in-run. As with leaping to punch a falling ball (figure 2b), ski-jumping requires precise timing of the start and duration of the jump action to fit the time to closure of the action-gap to the goal point (the lip of the in-run). Film analysis of fourteen ski-jumpers (Lee et al 1982) showed that they fitted the jump action into a precise spatio-temporal slot, which ended as their feet reached the lip of the in-run, by starting the jump action at a regular time ( $194 \pm 10$ ms) before the lip. The results are consistent with them using the tau of the action-gap to the lip to guide the jump action.

Long jumping requires similar timing skill. Figure 2d shows a long-jumper zeroing-in on the take-off board. Film analysis of athletes' footfalls showed that they visually regulated the lengths of their last few steps to the board (Lee et al 1982). At that stage in the run-up they were moving at a quite constant speed, and so tau of the action-gap to the board would have accurately specified the time to reach the board. What the long-jumper has to do is regulate the *durations* of their remaining steps to precisely fit the time to reach the board (as specified visually by tau), much as a dancer has to regulate the durations of their steps to fit the temporal constraints of the music. We hypothesized that this is achieved by adjusting the flight times rather than the contact times of the steps (step time equals flight time plus contact time), but we were unable to adequately test the hypothesis on the long jump data because the film frame rate (125 Hz) was too low. Therefore, another study was run where the movements of runners' limbs were measured at 312 Hz using Selspot motion capture equipment (Warren et al 1986). Participants ran at about  $4\text{ms}^{-1}$  on a treadmill and had to step on irregularly spaced patches (pretend stepping stones) on an extension to the treadmill belt (figure 2e). It was found that they regulated their step lengths to land on the patches principally by adjusting the flight times of the steps. Since the flight time of a step is proportional to the vertical component of the impulse delivered to the body

when thrusting from the ground, the results are consistent with the runners adjusting the vertical impulses so their steps fit the time to reach the upcoming mark, as specified by the tau of the action-gap to the mark.

Crossing the road often involves fitting the action of crossing into the spatio-temporal slots between oncoming traffic. Figure 2f shows a pretend road set-up designed to give children practice in road crossing (Lee et al 1984). The child looks along the real road and imagines there are corresponding vehicles on the pretend road. When the child judges it is safe to cross they walk across the pretend road. There are two action-gaps involved in making this decision: m-gL and m-gR, between the left and right vehicles and the crossing line (figure 2f). If the vehicles are travelling at constant speeds, then the difference between the taus of these two action-gaps equals the duration of the up-coming spatio-temporal slot that is available for crossing. If the time-to-cross is less than this spatio-temporal slot then safe crossing is possible, provided the child makes efficient use of the spatio-temporal slot by starting to cross right after the first vehicle has passed. This requires anticipating the arrival of the vehicle at the crossing line. Altogether the task might appear too complex for children. Yet, after only about an hour's guided practice spread over several sessions five year olds were performing nearly as well as adults in making efficient use of the spatio-temporal slots, particularly in single lane crossing where the spatio-temporal slot is between vehicles travelling in the same direction (Young and Lee 1987). The results suggest that the pretend road set-up would be a valuable addition to road safety programmes since it allows children to safely develop their skills in a real-life setting.

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## **7 General tau theory: initial questions**

The early tau studies were concerned solely with visual guidance, but in the late 80s my early interest in echolocation was renewed and this got me thinking about how tau might generalize. If actions can be visually guided by tau, might they not also be acoustically guided by tau - or indeed by tau information from *any* perceptual system? And might not the closure of *any* kind of action-gap (distance, angle, force etc) be guided by tau information? Also, might not the component movements of an action be coordinated with each other and with external events using tau? Pondering these

questions led me to the idea of *tau-coupling action-gaps*, which lies at the root of general tau theory.

## 8 Tau-coupling action-gaps

Two action-gaps,  $x$  and  $y$ , are said to be tau-coupled if the taus of the action-gaps remain in constant ratio during a period of time, i.e.,

$$\tau(x) = k\tau(y) \quad (2)$$

for a constant  $k$  (the coupling constant). Bearing in mind the general definition of an action-gap as the changing gap between two states (section 3.1), the action-gaps that are tau-coupled can be of different sorts. For example they may be *extrinsic action-gaps*, in the sense that they are perceivable by an observer from outside the animal; or *sensory action-gaps*, meaning that they are aspects of sensory arrays; or *intrinsic action-gaps*, in the sense that they are intrinsic to the animal (e.g., in its nervous system); or any combination of these. Let us start with some examples of actions involving tau-coupling of extrinsic action-gaps. The actions also involve extrinsic-sensory and extrinsic-intrinsic tau-couplings, which I shall discuss in later sections.

Figure 3 about here

## 9 Extrinsic-extrinsic tau-coupling

A bat landing on a perch needs to control simultaneously the closures of two extrinsic action-gaps: the *distance* action-gap,  $X$ , between itself and the perch, and the *angular* action-gap,  $A$ , between the direction line to the perch and the direction that line should assume during the final approach to the perch (figure 3a). The distance action-gap  $X$  needs to be closed properly to avoid crashing into the perch: the angular action-gap  $A$  needs to be closed properly to approach the landing from the right direction so that the bat can somersault and land upside-down. A film analysis of a bat performing this remarkable feat indicated that it controlled its flight by tau-coupling the extrinsic

action-gaps A and X, i.e., it kept  $\tau(A) = k\tau(X)$  for a constant k during the manoeuvre. At the same time, it controlled the deceleration of action-gap X by keeping tau-dot of X constant (Lee et al 1995).

Raising food to the mouth involves similar extrinsic/extrinsic tau-coupling. The hand has to stop at the mouth and approach it from the right direction (figure 3b) to avoid accidents like ramming the food up the nose. It was found that r, the distance action-gap to the mouth, and  $\alpha$ , the angular action-gap to the intended direction of final approach, were tau-coupled; i.e.,  $\tau(\alpha) = k\tau(r)$  for a constant k (Lee et al 1999). At the same time, the person controlled the acceleration and deceleration of action-gap r by intrinsically guiding the closure of the action-gap (section 13).

Tau-coupling also applies when intercepting a moving target. In one study, a ball was rolled down a track at about constant speed toward a 3-4 year old child (figure 3c). Hanging just to the side of the track was a bat. The child had to strike the bat with the hand just as the ball reached the bat. If successful, the ball went off the track and knocked down a pile of cans, causing great glee. It was found that the children tau-coupled the action-gap between their hand and the bat with the action-gap between the ball and the bat (van der Weel et al 1996; Lee et al 1997). In a later experiment, the target to be intercepted was moved at non-constant speeds to test whether tau-coupling also occurred under these conditions. Adults had to move a hand cursor vertically up a computer screen by means of a joystick so that the cursor stopped in a goal zone just as a target cursor, moving in a straight line from the bottom left or right of the screen with unpredictable constant acceleration or constant deceleration or constant speed, reached the goal zone (figure 3d). Here the possibly relevant action-gaps are between hand and goal, hand and target, and target and goal. Analysis of the trajectories of the hand and the target indicated that the participants moved the hand cursor so that the hand-goal and hand-target action-gaps were tau-coupled; that is, for a constant k, they kept  $\tau(HGgap) = k\tau(HTgap)$ .

Figure 4 about here

## 10 Sensing tau

A central principle of animal movement is that *the perceptual information guiding movement must extrapolate the movement into the future and must be readily available* (section 2). Tau affords extrapolation of a movement but is tau information readily available? Fortunately for animals it is - through extrinsic-sensory tau-coupling. This is because there are naturally occurring tau-couplings between extrinsic action-gaps and action-gaps in sensory flow fields, by virtue of physical power law relations between extrinsic and sensory motion gaps. For if two variables,  $x$  and  $y$ , are related by a power law of the form  $y = Cx^k$ , where  $C$  and  $k$  are constants, then it necessarily follows that  $\tau(x) = k\tau(y)$ ; the converse is also true, tau-coupling implies a power law relation<sup>5</sup> (Lee et al 1992a). I shall refer to this as the *power-law/tau-coupling duality*. Thus, if there is a power law relation between an extrinsic and a sensory action-gap, tau of the extrinsic action-gap can be sensed directly as a multiple of the tau of the sensory action-gap.

### 10.1 Monocular linear movement

Forward linear movement of the point of observation  $O$  generates an optic flow-field that moves with  $O$  (figure 4). The extrinsic action-gap  $Z_T$ , between  $O$  and the frontal plane containing the arbitrary point  $T$ , is power-law related (exponent = -1) to the sensory action-gaps  $x_T$  and  $y_T$  (equations (14) and (15), section A1.1). Therefore, from the power-law/tau-coupling duality:

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<sup>5</sup> The proof is straightforward. (i) If  $y = Cx^k$ , where  $C$  and  $k$  are constants, then differentiating with respect to time,  $\dot{y} = Ckx^{k-1}\dot{x}$ . Hence,  $\tau(y) = y/\dot{y} = (1/k)(x/\dot{x}) = (1/k)\tau(x)$ . (ii) If  $\tau(y) = (1/k)\tau(x)$ , then by definition,  $\dot{y}/y = k(\dot{x}/x)$ . Integrating we obtain  $y = Cx^k$ , where  $C$  is a constant.

$$\tau(Z_T) = -\tau(x_T) = -\tau(y_T) = -\tau(r_T) \quad (3)$$

There is much evidence that information about  $\tau(Z_T)$  (equation (3)) can be picked up monocularly, independently of information about the size and velocity of closure of the action-gap (e.g. Kaiser and Mowafy 1993; Kim et al 1993; Regan and Hamstra 1993; Gray and Regan 2004).

Sideways and vertical movement of O likewise generate optic flow-fields at O that move with O, and the basic geometry is the same as in figure 4b. However, for sideways and vertical movements of O, respectively, the extrinsic action-gaps  $X_T$  and  $Y_T$  are power-law related (exponent = +1) to the sensory action-gaps  $x_T$  and  $y_T$  (equations (14) and (15), section A1), and so from the power-law/tau-coupling duality:

$$\tau(X_T) = +\tau(x_T) \quad (4)$$

$$\tau(Y_T) = +\tau(y_T) \quad (5)$$

In all cases the direction of T is optically specified by the ratio  $x_T/y_T$ .

## 10.2 *Other perceptual systems*

The above principles apply not only to vision but also to any perceptual system that can register the changing directions of aspects of the environment relative to an animal when the animal moves and/or when objects move. In vision, direction is perceptible by virtue of the optic geometry of the eye, whether the eye consists of a lens and retina as in mammals or a radial bundle of ommatidia as in insects. In hearing, direction is

perceptible by virtue of the sonic geometry of the head and ears. This results in patterns of multiple sound reflections in the pinnae and time and intensity differences at the two ears, which together provide information about the directions of sound sources and surfaces that are reflecting sound (Batteau 1968). In olfaction, direction is perceptible by virtue of the geometry of the head and nose, which leads, e.g., to time and intensity differences in the two nostrils (von Békésy 1967). In haptics, direction is perceptible by virtue of the geometry of the body and the array of touch receptors in the skin.

### 10.3 *Binocular linear movement*

Considering now binocular vision, forward linear movement of the head generates two optic flow-fields, at the points of observation of the eyes,  $O_L$  and  $O_R$  (figure 4c). The extrinsic action-gap  $Z_T$ , between  $O_L$  and  $O_R$  and the frontal plane containing the arbitrary point  $T$ , is power-law related (exponent = -1) to the sensory action-gaps  $x_L$  and  $y_L$  in the left eye's optic flow-field, and  $x_R$  and  $y_R$  in the right eye's optic flow-field (equations (28) to (31), section A1.2). Therefore, from the power-law/tau-coupling duality,  $\tau(Z_T)$  is specified in each eye separately by

$$\tau(Z_T) = -\tau(x_L) = -\tau(x_R) = -\tau(y_L) = -\tau(y_R) \quad (6)$$

$\tau(Z_T)$  is also specified in the two eyes together (section A1.2) by

$$\tau(Z_T) = -\tau(x_L - x_R) \quad (7)$$

$$\tau(Z_T) = -\tau(y_L + y_R) = -\tau(x_L + x_R) \quad (8)$$

Equation (7) corresponds to binocular disparity, equation (8) to binocular concordance (Jones and Lee 1981). In studies of judgment of time to contact in the Z direction, using displays where distance and velocity information is excluded, Gray and Regan (2004) have shown that  $\tau(Z_T)$  is perceivable both monocularly (equation (3)) and through binocular disparity alone (equation (7))<sup>6</sup>. They also give evidence that when monocular and binocular disparity and concordant information about time to contact are combined the accuracy of pick-up of  $\tau(Z_T)$  is enhanced.

Sideways and vertical movement of the binocular points of observation likewise generate optic flow-fields at  $O_L$  and  $O_R$ . For sideways movement,  $\tau(X_T)$  is specified through binocular concordance (section A1.2) by

$$\tau(X_T) = \tau(x_L + x_R) \quad (9)$$

For vertical movement,  $\tau(Y_T)$  is specified through binocular concordance (section A1.2) by

$$\tau(Y_T) = \tau(y_L + y_R) \quad (10)$$

#### 10.4 *Tau specified through inverse square power laws*

So far we have discussed two simple common power law relations between an extrinsic action-gap,  $E$ , and a sensory action-gap,  $s$ , namely  $s = \alpha E^{-1}$  and  $s = \alpha E$ , where  $\alpha$  is a

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<sup>6</sup> Equation (7) is equivalent to equation (12) of Regan and Gray (2004).

constant. These lead to the respective tau specifications:  $\tau(E) = -\tau(s)$  and  $\tau(E) = \tau(s)$ . Another common power law in nature is the inverse square law. If  $E$  and  $s$  are related by an inverse square law then  $s = \alpha E^{-2}$  (for constant  $\alpha$ ) and so the tau specification is  $\tau(E) = -2\tau(s)$ . For example, the intensity of sound,  $i$ , at the head is, to a good approximation, proportional to the inverse square of the distance from the source of the sound. Thus,  $i = \alpha E^{-2}$  and so  $\tau(E) = -2\tau(i)$ . There is evidence in humans for the acoustic pick-up of  $\tau(i)$  in judging time to closure of an action-gap with a sound source (Schiff and Oldak 1990; Rosenblum et al 1993). Other examples of the inverse square law, or at least a good approximation to it, are the intensity of a chemical or infra-red radiation or electric field at a distance from the source of the energy. Thus, animals that guide their movements by sound - e.g. bats (Griffin 1958), dolphins (Houser et al 2005); or by smell/chemotaxis - e.g., microbes (Armitage 1999); or by infra-red radiation - e.g. rattle-snakes (Newman and Hartline 1982); or by electric fields - e.g., weakly electric fish (Bastian 1986), sharks (Kajiura and Holland 2002), platipi (Manger and Pettigrew 1995), bacteria (Adler and Shi 1988) - all could, in principle, exploit the inverse square law to sense, through the tau of the intensity action-gap,  $i$ , at their perceptual organs, the tau of the extrinsic action-gap,  $E$ , to the source of the stimulation, and thus guide themselves to the source. In each case the extrinsic-sensory tau-coupling they could use is  $\tau(E) = -2\tau(i)$ . The extent to which animals do guide their movements in this way is an empirical question that needs to be investigated.

## 11 Action-scaling space

In addition to the temporal information afforded by tau, an animal also needs spatial information. It needs information about the directions in which objects lie, and it needs information about spatial extent - e.g., about the width of a gap it wants to jump. This would appear to pose a problem because distance is not directly specified in the optic flow-field, only relative distance (equations (14) - (19)). However, it is not information about the width of the gap in metres or any other arbitrary unit of measure that it needs,

but rather information for *action-scaling* the width of the gap (Lee 1980; Lee 1993; von Hofsten & Lee 1994). It requires, for instance, information about the magnitude of leg thrust needed to clear the gap. In general, the environment and objects in it need to be perceived in terms of the type and magnitude of action that could or is to be applied<sup>7</sup>. The following are some ways this might be achieved.

### 11.1 *Action-scaling by eye-height*

Referring to figure 4b,  $G(0, Y_G, Z_G)$  is an arbitrary point on the ground beneath the OZ axis. Therefore  $-Y_G$  equals the person's eye-height. When the eye is moved in the direction OX or OY or OZ, the spatial coordinates  $(X_T, Y_T, Z_T)$  of the arbitrary point T, and the velocity and acceleration of the eye are all optically specified in terms of eye-height  $Y_G$ , tau and direction (section A1.3). Thus eye-height can be used in action-scaling space. If a person were to do this, then artificially lowering eye height, unbeknown to the person, should make speed, distances and sizes appear larger. The principle was used to dramatic effect in the movie "The Incredible Shrinking Man" (1957). By placing the camera that created the audience's eye view close to the floor in a doll's house, the house was made to appear the size of a normal house and a cat peering in the window looked enormous. This effect has been studied in two experiments. Standing subjects viewed a variable width doorway (Warren and Whang 1987) or steps (Mark 1987) through an aperture that prevented them seeing that the floor on which the doorway or steps stood was higher than the one on which they stood. The result was that the subjects perceived the doorway to be wider and the steps higher than they actually were.

### 11.2 *Action-scaling by locomotor cycles*

Natural locomotor activity is generally cyclical, whether on the ground, in water or in the air. The frequency of strides, wing-beats or tail-beats tends to be regular, though can be changed to fit in with the demands of the environment. Suppose an animal is moving

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<sup>7</sup> This relates to the concept of affordance (Gibson 1979).

linearly at a constant speed with a constant locomotor cycle time  $T_L$  that produces regular locomotor displacements of the body forwards. Consider for example the person depicted in figure 4a. If at the start of a locomotor cycle (when, say, the right foot leaves the ground) the tau of the action-gap to the frontal plane containing the tree is  $\tau(Z_T)$ , then the size of the action-gap is  $(\tau(Z_T)/T_L)$  locomotor units (strides in this case).  $T_L$  is optically specified as the difference between the values of  $\tau(Z_T)$  at the start of successive locomotor cycles. It then follows (section A1.5) that the spatial coordinates  $(X_T, Y_T, Z_T)$  of the arbitrary point T are optically specified by tau and direction in locomotor units. Visual regulation of the locomotor cycle to land on stepping stones or to hit the take-off board when long jumping (section 6) could utilize this type of information. In each case the runner could adjust the locomotor cycle time to control where the foot lands by regulating the power of the thrust applied to the ground. Birds and fish might also use the same type of information when adjusting their wing-beats or tail-beats, e.g., when preparing to pass through a narrow opening.

### 11.3 *Action-scaling by head acceleration*

Systematic movement of the head when preparing for action is a common phenomenon. For example, cats often bob their heads when preparing to leap, as do pigeons when walking or flying to a perch (Davies & Green, 1988). Goalkeepers preparing for a penalty shot and tennis players waiting to receive a serve also often move their heads systematically. Why do they do this? A possible answer is that they action-scale space through the acceleration of their head (which they register, e.g., through their vestibular system). The spatial coordinates  $(X_T, Y_T, Z_T)$  of the arbitrary point T are optically specified by tau and direction in terms of the acceleration of the head (section A1.6). This type of action-scaling may be a contributing factor in the motion-sickness frequently experienced in flight and driving simulators, where the acceleration of the head does not match the displayed visual information about the locomotion of the body.

(Figure 5 about here)

## 12 Steering

### 12.1 *Steering optic flow-fields*

So far we have mainly considered movement along a straight line. Let us now consider locomotion along a curve, starting with a circular arc (Lee and Lishman 1977). Figure 5a(A) shows the optic flow field (dashed lines) at a driver's eye when travelling straight down the middle of a one-way road, the edges indicated by solid lines. (The image is the projection onto a plane orthogonal to the direction of travel, as in figure 4b.) The central heavier dashed line is the 'locomotor flow line' that specifies the vehicle's potential course, if the lateral force remains constant at zero. The line meets the edge of the road at the bend. The tau of the action-gap to that point is optically specified in the optic flow field (as in figure 4b), providing the driver with information for timing the steering adjustment to negotiate the bend. Figure 5a(C) again shows a linear course, but this time the potential course intersects the left-hand edge of the road before the bend. Again tau provides information for timing the steering adjustment to bring the vehicle back on course. Figure 5a(B, D) show related situations, except that the vehicle is on a circular course and so the flow lines are projections of concentric circles. In figure 5a(B) the vehicle's potential course, if the lateral force on it remains constant, is specified by the locomotor flow line, which lies down the middle of the bend. In figure 5a(D) the potential course goes off the road to the left before the bend. In this case, the tau for timing the steering adjustment is specified differently to the linear case, as explained below.

### 12.2 *Tau on circular courses*

Figure 5b shows a point of observation O on a circular course (Lee 1998). G is an arbitrary point on the course. R is a distant reference point, e.g., on a tree. Thus the line OR serves as a reference direction, like a compass bearing. OR is in the plane of motion and lies angularly close to the instantaneous direction of motion OM, i.e., angle ROM is small. (The distant reference point R may be periodically changed during the motion to

keep angle ROM small.) The tau of the *reference angle*  $\Theta_{\text{ROG}}$  between OR and OG, and the tau of the *motion angle*  $\Theta_{\text{MOG}}$  between the instantaneous direction of motion OM and OG, are both relevant to steering a circular course. When G is on the circular course, as in figure 5b, then (writing  $\tau_{\text{MOG}} = \tau(\Theta_{\text{MOG}})$  etc.),  $\tau_{\text{MOG}} + \tau_{\text{ROG}} = 0$ . If G were off the course on the outside then  $\tau_{\text{MOG}} + \tau_{\text{ROG}}$  would be greater than zero; if G were off the course on the inside then  $\tau_{\text{MOG}} + \tau_{\text{ROG}}$  would be less than zero (Lee 1998). Thus the potential circular course, if lateral force remained constant, is specified by the set of points for which  $\tau_{\text{MOG}} + \tau_{\text{ROG}} = 0$ . In an experiment in a locomotion simulator, direction of circular heading with respect to a destination point was perceived to an accuracy of  $1.5^\circ$  (Warren et al 1991). The participants could have been using the tau information just described.

When steering a circular arc course along a road,  $\tau_{\text{MOG}}$  could also be used to (a) time steering adjustments if the potential course were threatening to wander off a road and (b) control braking along the circular arc. This is because  $\tau_{\text{MOG}}$  for a point G on the arc equals the tau of the action-gap along the circular arc between O and G (Lee 1998). Thus, (a) if the potential circular course intersects the edge of the road at G,  $\tau_{\text{MOG}}$  provides information for timing steering adjustments, and (b) braking to stop at G could be guided by keeping  $\dot{\tau}_{\text{MOG}}$  constant (Section 4)<sup>8</sup>.

### 12.3 Steering around bends

A course may be steered around a bend using just  $\tau_{\text{MOG}}$  by taking the (moving) tangent point on the inside edge of the bend as G, as shown in figure 5c, top (Lee 1998). Suppose the bend is on a one-way road and is of constant curvature, as many road bends are. Then keeping  $\tau_{\text{MOG}}$  infinite (i.e.,  $\Theta_{\text{MOG}}$  constant) would result in the vehicle keeping a constant distance from the inside edge of the road or lane, by following a circular path with the same centre of curvature. Racing drivers, on the other hand, swing into bends, as do most

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<sup>8</sup> Keeping tau-dot constant is equivalent to intrinsic guidance by tau-coupling (section 13)

drivers to a certain extent. This requires decreasing  $\Theta_{\text{MOG}}$  to a lower value,  $\Theta_{\text{MOG}}^*$  say, when rounding the bend (figure 5c, bottom). The task could be solved by keeping  $\dot{\tau}(\Theta_{\text{MOG}} - \Theta_{\text{MOG}}^*)$  constant at a value less than 0.5 (Section 4)<sup>8</sup>. Drivers tend to fix gaze on the tangent point as they approach and enter a bend (Land and Lee 1994). This could facilitate the pick-up of  $\dot{\tau}(\Theta_{\text{MOG}} - \Theta_{\text{MOG}}^*)$ .

#### 12.4 *Asymptoting on surfaces*

Consider the problem of steering to a flat surface and arriving moving parallel to it (Lee 1998). Examples are a bird or airplane pilot landing on the ground or water, or a driver straightening out of a bend. Figure 6d diagrams two versions of the problem: first (top diagram) where the contact point is specified, and second (bottom diagram) where it is unspecified. In the first case, as O reaches the goal G and  $D_G$  becomes zero, the angle  $\Theta_{\text{OGS}}$  also has to reach zero. In principle, this could be achieved by coupling  $\tau_{\text{OGS}}$  (the tau of  $\Theta_{\text{OGS}}$ ) and  $\tau_G$  (the tau of  $D_G$ ). Sensing  $\tau_{\text{OGS}}$  would seem to pose a problem, but it turns out not to be necessary. It would be sufficient to couple  $\tau_{R'}$  and  $\tau_G$ , both of which could, in principle, be sensed (Section 10). This tau-coupling, when angle  $\Theta_{\text{OGS}}$  is small, would automatically ensure that  $\tau_{\text{OGS}}$  and  $\tau_G$  were coupled<sup>9</sup>. Asymptoting at an unspecified point (figure 5d, bottom) could be solved in a similar way by coupling  $\tau_{R'}$  and  $\tau_{M'}$ . When

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<sup>9</sup> Proof. Applying the sine rule to triangle OPG in figure 5d (top) gives  $D_R \sin \Theta_{\text{OGS}} = D_G \Theta_{\text{OGS}}$ . Differentiating the equation with respect to time and eliminating  $\dot{\Theta}_{\text{OGS}}$  (which is constant) between the two equations yields  $1/\tau_{R'} = 1/\tau_G + 1/\tau_{\text{OGS}}$ . Thus, if  $\tau_{R'}$  and  $\tau_G$  are coupled, by keeping  $\tau_G = k\tau_{R'}$  for a constant  $k$ , then eliminating  $\tau_{R'}$  between the two equations gives  $\tau_G = (k-1)\tau_{\text{OGS}}$ . That is,  $\tau_G$  and  $\tau_{\text{OGS}}$  are tau-coupled. Similar reasoning applies to figure 5d(lower) in proving that  $\tau_{\text{OM'S}}$  and  $\tau_{M'}$  are tau-coupled.

angle  $\Theta_{OM'S}$  is small, this ensures that  $\tau_{OM'S}$  and  $\tau_M$  are coupled, which would make the angle of approach to the surface zero at contact.

### 12.5 *Steering to a goal*

This may be guided just in terms of  $\tau_{MOG}$  (Lee 1998). As a simple example, keeping  $\tau_{MOG}$  infinite (equivalent to keeping  $\Theta_{MOG}$  constant) would result in the animal moving along an equi-angular spiral toward the goal at the origin (figure 5e, top). Insects have been observed to follow such a spiral toward a candle (Buddenbroek, reported in Thompson, 1966). Pilots of light aircraft use the procedure to spiral down to an airstrip, by keeping a mark on the windshield in line with a landing point. Although the procedure theoretically requires an infinite number of circuits to reach the goal, for practical purposes we need simply consider getting in range of the goal and then breaking out of the spiral. Moving more directly to a goal could be achieved by shifting the centre of outflow in the sensory flow field to within the goal area, stopping it there and keeping it there. (Imagine steering a car until the headlight beam settles on a destination.) This means closing the motion angle  $\Theta_{MOG}$  so that its closure-rate tends to zero as it tends to zero, which could be achieved by starting  $\Theta_{MOG}$  reducing and then keeping  $\dot{\tau}_{MOG} = k$  for a constant  $k$  between zero and 0.5 (Section 4). The consequence of doing this is illustrated in figure 5e (middle). The course swings around, reducing the motion angle  $\Theta_{MOG}$  at a decelerating rate, until the course settles on a straight line toward the goal with  $\Theta_{MOG} = 0$ .

### 12.6 *Steering to a goal and stopping*

This could be achieved by a single tau-coupling, namely  $\tau_G = k\tau_{MOG}$ , for constant  $k$ ,  $0 < k < 1$ , as shown in figure 6e, bottom (Lee 1998). The tau-coupling would ensure that as the angular action-gap  $\Theta_{MOG}$  tended to zero the distance action-gap  $D_G$  would tend to zero and at the goal its closure-rate would be close to zero. Specifically, for  $0 < k \leq 0.5$ , the

closure-rate of  $D_G$  would tend to zero at the goal, whereas for  $0.5 < k < 1$  there would be some residual closure-rate as the goal was reached. The value of  $k$  would also affect the shape of the path to the goal, as shown in figure 5e (bottom).

### 12.7 Arriving from the right direction and stopping

It is often necessary to arrive at place from the right direction and control speed at the same time. A driver turning into a narrow parking place and a bird flying into a nesthole both face this problem, and usually solve it quite accurately. How is it done? In Section 6 and figure 3a,b two experiments are described - on bats landing on a perch and on humans raising food to the mouth - which indicate that one way of arriving at a goal from the right direction and stopping there is to simultaneously tauG guide (section 13) the distance action-gap to the goal and tau-couple the distance action-gap to the goal with the angular action-gap formed by the current direction line to the goal and the aimed for direction line of final approach.

## 13 Intrinsic-cum-perceptual guidance of movement

The third principle of animal movement (section 2) is that *movement requires constant intrinsic-cum-perceptual guidance*. I have discussed perceptual guidance of action-gaps but what about their intrinsic guidance? For example, how does a peregrine falcon modulate its bill action when changing from tearing at a carcass to gently feeding the food to its young? Or how does a pianist control expression by varying finger action? For intrinsic guidance to coordinate with perceptual guidance the two must communicate. If perceptual guidance talks the language of tau, then intrinsic guidance should do likewise. A few years ago (Lee 1998), I proposed that an animal intrinsically-cum-perceptually guides the closure of an extrinsic action-gap by generating in its brain an intrinsic action-gap (possibly between electrical energy levels) and regulating its muscles, while constantly perceptually monitoring the tau of the extrinsic action-gap, so that the extrinsic action-gap remains tau-coupled to the intrinsic action-gap, such that

$$\tau(\text{extrinsic action-gap}) = k\tau(\text{intrinsic action-gap}) \quad (11)$$

Here  $k$  is constant during any particular action-gap closure, but can be varied by the animal between action-gaps to modulate the dynamics of the movement.

(Figure 6 about here)

What form might an intrinsic action-gap follow? Two types of extrinsic action-gap guidance may be distinguished. The first involves guiding just the deceleration of a closing action-gap, as when a driver brakes to stop at an obstacle, or a bird slows down to land on a perch. The second involves guiding the acceleration and then the deceleration of an action-gap (e.g., the action-gap between the hand and a glass when reaching from rest for the glass), or guiding the acceleration and deceleration of an action-gap twice over, as when repeating a note on a xylophone, which entails first opening and then closing the action-gap between the hammer and the key. The first type of guidance (deceleration only) was discussed in section 4, in terms of keeping  $\tau$ -dot constant. The second type (acceleration and deceleration) is described in Lee et al (2005b). Both types can be understood in a unified way as involving intrinsic action-gaps in the nervous system that close with either constant acceleration or constant deceleration. The idea can be explained in terms of a bouncing ball (figure 6a). Under gravity, the ball moves towards its zenith under constant deceleration and toward the ground under constant acceleration. The intrinsic action-gap,  $G$ , for acceleration-plus-deceleration guidance corresponds to the constant acceleration action-gap between the ball and the ground. The intrinsic action-gap,  $D$ , for deceleration-only guidance corresponds to the constant deceleration action-gap between the ball and the zenith. The tau formulae of the intrinsic action-gaps  $G$  and  $D$  are obtained by applying Newton's equations of motion to the bouncing ball (Lee 2005), whence the following tau-coupling equations between an extrinsic action-gap,  $X$ , and  $G$  and  $D$  are derived:

$$\tau(X) = k\tau_G = kt(T + t)(T + 2t) \quad (12)$$

$$\tau(X) = k\tau_D = kt/2 \quad (13)$$

Here time,  $t$ , is zero at the goal (ground for G, zenith for D),  $T$  is the total duration of movement of the ball from the ground through the zenith and back to the ground, and  $k$  is the coupling constant that stays fixed during a movement. These two types of intrinsic tau guidance will be referred to as *tauG guidance* and *tauD guidance*. (N.B the time derivative of the tauD guidance equation (13) is  $\dot{\tau}(X) = k/2$ , and so tauD guidance is equivalent to tau-dot guidance of deceleration (section 4).) It should be stressed that tauG and tauD guidance do not necessarily commence when the intrinsic action-gap starts changing: an extrinsic action-gap may be tau-coupled onto an intrinsic action-gap during the course of the intrinsic action-gap. This possibility is indicated in figure 6a by the different coloured arcs.

Figure 6 shows also how the size and velocity of an extrinsic action-gap,  $X$ , change over time as a function of  $k$  when the action-gap is tauG guided (figure 6b,d) or tauD guided (figure 6c,e). In each case, the higher the value of  $k$ , the more abrupt is the final approach to the goal. For  $0 < k \leq 0.5$ , the final approach is decelerative and gentle, the gap velocity reaching zero at the goal. For  $0.5 < k < 1$ , the final approach is decelerative and progressively harsher the higher the value of  $k$ ; and the gap velocity does *not* reach zero at the goal. For  $1 < k$ , the final approach is accelerative and gets progressively harsher as  $k$  increases. In general, velocity at the goal is zero if  $k \leq 0.5$ , and increases monotonically with  $k$  when  $k > 0.5$ .

One experimental example of tauG guidance of movement is raising food to the mouth (figure 3b): the action-gap between the hand and mouth was found to be tightly tauG guided<sup>10</sup> (Lee et al 1999). Other examples are the following.

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<sup>10</sup> The  $\tau(X) = k\tau_G$  hypothesis is tested by linearly regressing  $\tau(X)$  on  $\tau_G$ . The movement is considered to be tightly tauG guided if  $r^2 > 0.95$ , meaning that over 95% of the variance in the data is accounted for by the hypothesis. The regression slope is then taken as the measure of  $k$ .

(Figure 7 about here)

## **14 TauG guidance by infants**

### *14.1 Nutritive sucking*

Figure 7a illustrates an early example of tauG guidance - a full-term newborn baby sucking milk out of a bottle (Craig and Lee 1999). The graphs show how the intra-oral pressure (recorded via a catheter passing through the teat into the mouth) and its time derivative, pressure velocity, varied smoothly and systematically during a typical suck. As the baby drew in milk the pressure action-gap closed to the lowest pressure; as the baby relaxed sucking the action-gap opened ready for the next suck. The tau of the pressure action-gap during suction was calculated from the pressure and pressure velocity curves and tested against the tauG formula to see whether the sucking action was tauG guided. It was found to be tightly tauG guided<sup>10</sup> - as tightly, in fact, as an adult's reaching (Lee et al 1999). Thus babies can be born already able to use tauG guidance. This implies that, in general, they have the potential to tauG guide their actions, though their ability to do so doubtless depends on practice, as with any skill. In the case of sucking, they might have practised tauG guidance in the womb, as is suggested by ultrasound recordings of foetuses sucking their fists and the amniotic fluid.

### *14.2 Gesturing*

Early arm and leg movements also are tauG guided. Figure 7b shows a 10-week-old baby gesturing with arms and legs when music was playing<sup>11</sup>. The baby is supported in a special seat with its chest resting against the seat and its arms and legs free to move - like being supported against a shoulder. The movements of the baby's arms and legs, recorded by motion-capture cameras, were found to be tightly tauG guided. This precise tauG guidance of the arms and legs relative to the body in a 10-week-old is in sharp contrast

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<sup>11</sup> Study carried out by K Hooker and J Perkins for their Honours Dissertations in Psychology, Edinburgh University, 2003.

with the imprecise and jerky guidance of the hands in infants younger than about 18 weeks, when reaching for stationary and moving objects starts (von Hofsten 1983). This difference might be due to the different perceptual information used: the perceptual information for guiding gestures comes mainly through the receptors in the joints and muscles, whereas in reaching for a seen object visual information plays a major role.

## **15 TauG guidance of gaze**

All actions are based on controlled movement of perceptual systems to pick up information for guiding the act. Vision normally involves moving the eyes together with the rest of the body. As Gibson (1979) elegantly put it, we see "with the eyes in the head on the shoulders of a body that gets about." Eye, head and body movements therefore need to be coordinated to direct gaze appropriately. Madeleine Grealy, Ben Schogler and I studied this coordination in an experiment that required the participant to first look over their shoulder and then turn to look at an object (up until then invisible) that was moving along a horizontal track in front of them. Figure 7c shows typical plots of the angle of the eye relative to the head, the head relative to the world, and the gaze (the line through the fovea and the nodal point of the eye's lens) relative to the moving object (Lee 2005). The different colours on the graph lines indicate segments from one zero velocity point to the next. Each coloured segment was tightly tauG guided. The segments of the head, eye and gaze movements overlap in time as do the parts in contrapuntal music.

## **16 TauG guidance by athletes**

### **16.1 *Putting***

To investigate how golfers control the length of their putt, we analyzed the club and ball movements of ten low-handicap players (Craig et al 2000). They all tightly tauG guided the movement of the club from the start to the end of the swing and increased the length of the putt mainly by increasing the length,  $D$ , of the swing and the  $k$  value in the tauG guidance equation (12), while keeping the duration,  $T$ , of the swing and the relative position,  $P_T$ , of the ball in the swing quite constant (figure 7d).

### **16.2 *Sprinting***

The contrapuntal flow of tauG guided movements found in the study of shifting gaze (section 15) came to light in an analysis of the limb movements of sprinters. Functionally important segments of the sprinters' movements were tightly tauG guided. As with the head-eye-gaze movements, these segments overlapped in counterpoint. Figure 7e illustrates this. It shows, for one of the sprinters, the movement of the right metatarsal relative to the right hip (marked at the top of the figure). Data points are every 4ms. The tauG guided segments of movement were: (1) the horizontal component of movement of the right metatarsal, both from 'back' to 'front', and from 'front' to 'back' (as marked on figure 7e) - important for ensuring that when the foot contacts the ground it is in the right horizontal position just in front of the hip to facilitate the thrust; (2) the forward (red bars) and the backward (blue bars) horizontal component of movement of the centre of gravity of the leg – important for enhancing the horizontal component of thrust from the other leg and the horizontal component of acceleration during flight; (3) the upward (orange and red dots) and the downward (blue dots) vertical component of movement of the centre of gravity of the leg – important for enhancing the vertical component of thrust from the opposite leg and the vertical component of acceleration during flight. (4) the extension of the right leg (metatarsal-hip distance) when thrusting off from the ground (green bars) – important for regulating the timing of the thrust. The vertical component of force on the body at foot contact and during flight was also regulated by tauG guiding the vertical component of movement of the centres of gravity of the arms (not shown).

In addition, the foot was tightly tauG guided *relative to the ground*. This is illustrated in figure 7f, where the colour code is the same as in figure 7e. The action-gap indicated by the straight black line was tauG guided. This guidance is important both for securing adequate footing (particularly important when the ground is rough) and for ensuring that the velocity of the foot relative to the ground is close to zero at touch down, because if the foot were moving forward at touch-down this would retard the body.

Sprinting is thus a finely orchestrated contrapuntal flow of tauG guided movements. This is not to say that the parts always blended perfectly. Our analysis revealed sections of the sprinting movement that could benefit from finer tauG guidance. Thus, general tau theory not only provides new insight into the art of sprinting but also offers ways of improving performance.

## **17 TauG guidance in performing music**

### *17.1 Timing*

Timing is a crucial aspect of playing in a group. The margin for error between players is only about 20ms. Achieving such precision requires a fine degree of prospective control. However, it is not like catching a ball where there is continuous visual information available about the approach of the ball. Rather the information for synchronising with the next beat needs to be in the performer's head. Craig, Pepping and Grealay (2005) investigated the process in an experiment where the participant moved a cursor between two target zones on a computer screen to coincide with sounded beats. Their results indicated that for inter-beat intervals up to 3s the participant generated intrinsic tauG guides to bridge the intervals between beats, and coupled the tau of the action-gap to the next target zone onto the intrinsic tauG guide.

### *17.2 Musical expression*

An essential aspect of music (and speech) is its expressivity, its ability to effectively convey thought and feeling (Clynes 1973). What is it in the pattern of flow of the music that communicates the underlying emotion that moves us? Music is a continuous ever-changing flow of sound, occasionally punctuated by staccato notes and pauses. The continuity of sound is important for understanding musical expression. To be sure, the flow of musical sound touches down on notes and chords, but even on these temporary dwelling places the flow is restive - the sound varies in loudness, pitch and timbre. The pattern of flow of sound fluctuates even more when moving between notes. Musical expression lies in the manner in which the flow of sound changes, both on and between notes. Musicians achieve expression by the way they *move* in modulating their vocal apparatus, drawing the bow across the strings, pressing the piano keys. Remarkably, the same musical expression can be achieved on different instruments using quite different movements (e.g., bowing vs key pressing). These, in turn, produce quite different sounds (violin vs piano). Furthermore, a person can pick up the feeling in the music and express it in gesture or dance. Therefore musical expression must be embodied in certain underlying expressive variables of the flow of movement and sound that are invariant

across different means of expressing the music (figure 8a).

Recently, we have applied general tau theory to understanding musical expression (Lee et al 2005; Lee and Schogler 2005). There are three parameters of a tauG guided movement:  $k$ , the coupling constant in the guidance equation (12);  $A$ , the amplitude of the movement; and  $T$ , the duration of the tauG guidance. Our working hypotheses were: (1) musicians tauG guide their movements and regulate the values of the parameters  $k$ ,  $A$ ,  $T$  to convey expression; (2) these movements generate tauG guided sounds with related, though not necessarily identical,  $k$ ,  $A$ ,  $T$  values; (3) these  $k$ ,  $A$ ,  $T$  values in the sound can be perceived and expressed, for example, as tauG guided gestures with related  $k$ ,  $A$ ,  $T$  values. In short, we hypothesize that  $k$ ,  $A$  and  $T$  are parameters of musical expression. The parameter  $T$  relates to pitch, rhythm and timing;  $A$  relates to sound intensity;  $k$  regulates the pattern of flow of the movement.

### 17.3 *Pitch-slides*

One study analyzed singing<sup>12</sup>. Amateur accomplished female singers sang a piece by Pergolesi ('Vanne, Vale, Dico Addio'). The singing was legato, which meant that when moving from one note to the next the voice slid through the range of pitches between the notes. This produced a pitch action-gap or 'pitch-slide' (figure 9b). The pitch-slides were recorded both acoustically and through a laryngograph. They were found to be tightly tauG guided. The  $k$  values were not significantly different for the acoustic and laryngograph records, indicating that the pitch-slides were produced by tauG guided movement in the larynx. However, the  $k$  values for musically unstressed pitch-slides were significantly lower than for stressed pitch-slides, though the durations ( $T$ ) and intensities ( $A$ ) did not differ significantly. This indicated that the parameter  $k$  was used by the singers to vary musical expression through the pitch-slides: the unstressed pitch-slides ended with a gentle deceleration, the stressed ones with a harsher deceleration.

Pitch-slides were also studied in trombone playing (figure 8c). A player produces pitch-slides by moving the trombone slide, and by regulating the tension in their lips. An

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<sup>12</sup> Study carried out by P Biggs and E Ward for their Honours Dissertations in Psychology, Edinburgh University, 2004.

amateur trombonist played a rapid pitch-slide between two notes a tone apart, both with and without moving the trombone slide. The pitch-slides produced by the trombone slide or by the lips alone were tightly tauG guided, as was the movement of the trombone slide itself, but there were no significant differences between the k values. Thus, the movements of the trombone slide, the lips and the resulting acoustic pitch-slide were all tauG guided with a similar k value.

Another pitch-slide study examined the relation between singing and the gestures that accompanied it (figure 8c). A professional jazz singer performed “The beat goes on” unaccompanied while her voice and hand gestures were recorded. Her pitch-slides and the hand movements that accompanied them were found to be tightly tauG guided. The k values were similar, though the hand movements lasted about twice as long as the pitch-slides. This indicates that the voice and hand were independently tauG guided, but used similar k values, presumably to express the same musical feeling.

#### 17.4 *Intensity-slides*

A further study investigated the expressive use of 'intensity-slides' in bass playing<sup>13</sup>. When a sound is made, the intensity evolves in three distinct phases: attack, sustain and decay (Galembo et al, 2001). In the attack phase, which contains information crucial to the character of the sound, the intensity of the sound rises rapidly to a peak level in what we call an 'intensity-slide'. The expressive use of intensity-slides is evident in all forms of music, perhaps most obviously in vocal and instrumental jazz. In the study, a professional bass player bowed a key phrase from Tchaikovsky's “The dance of the sugar plum fairy” several times in two moods, happy and sad (figure 8d). How the bow moved across a string modulated the intensity-slide (attack) on the note. The intensity-slides and the bow movements that produced them were tightly tauG guided. The k and T values were significantly higher in the sad mood, both for the sound and the bow movement. That is, the intensity-slides and bow movements were longer and ended more abruptly in the sad rendition of the musical phrase.

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<sup>13</sup> Study carried out by B Harvey and J Scriven for their Honours Dissertations in Psychology, Edinburgh University, 2004

## **18 Applying tauG therapeutically**

Parkinson's disease is one area of application of general tau theory. A striking aspect of the disease is paradoxical movement: a person may suffer extreme slowness of movement (bradykinesia) and/or freezing (akinesia) when attempting to make self-initiated movements like stepping off across a clear floor or reaching for a cup, but these symptoms can largely disappear when the person is in a more dynamic, and apparently more demanding situation, such as walking downstairs or catching a ball. In the first case the person is more reliant on intrinsic tauG guidance of their limb movements, whereas in the latter case their limb movements can be tau-coupled to extrinsic action-gaps such as the gap between themselves and the next stair or the gap between the approaching ball and the catching place. Therefore, if they could be given a 'tauG aid' it might help alleviate their problems with self-initiated movements. We have devised a sonic tauG aid that produces a tauG guided pitch-slide between two notes. The duration  $T$  and the  $k$  value of the pitch slide can be regulated to match the duration and style of the action to be aided - e.g., walking steps. Work is still in progress with the aid but preliminary results with walking and writing are promising.

Another potential application of general tau theory is in the diagnosis of neuro-developmental disorders in infants. TauG guided sucking in young infants has been used with some success in assessing such disorders (Craig et al 2000), as has the use, around thirty weeks of age, of tau in catching a moving toy (van der Meer et al 1995). Much more work needs to be done in this area.

## **19 TauG in the brain**

If movements are intrinsically guided by tauG, then presumably there is tauG-like information coursing through the nervous system. This nervous information is likely to be some (mathematical) function of 'neural power' - the rate of flow of electrical energy through ensembles of neurons, either as trains of electrical pulses or as action potentials - since the nervous system appears to function by modulating neural power. However, tauG could not correspond to neural power as such because the dimensions do not match - tauG is measured in time units whereas neural power is measured in power units. But tauG

could be encapsulated neurally as the *tau* of a neural power action-gap. The hypothesis was tested by analyzing neural power data collected from monkey motor cortex and parietal cortex area 5 during a reaching experiment. In each cortex a neural power action-gap was found whose 'tau melody' (the temporal pattern of tau) was proportional to the tauG melody and to the tau melody of the action-gap between the monkey's hand and the target as it reached. In the motor cortex, the neural tau melody preceded the hand movement tau melody by about 40ms, indicating that it was prescribing the movement. In parietal cortex area 5, the neural tau melody followed the movement tau melody by about 95ms, indicating that it was monitoring the movement. We are currently further testing the hypothesis on single unit recordings made in the basal ganglia of monkeys during a reaching task.

## **20 The future**

If there is a single take-home message from this article it must be that guiding movement purposively is the origin of being. All living creatures from the largest mammal to the tiniest microbe need to do this to live. Therefore to understand what it is to be alive we must understand how movement is guided. We need to grasp this at different levels - anatomical, physiological, neural, molecular, genetic - but first and foremost we need to understand it at the behavioural level. Only then can we ask informed biological questions at lower levels, and so avoid not seeing the wood for the trees.

I have described a theory of movement guidance - general tau theory. It was initially pitched at the behavioural level, but has since been generalized to cover (potentially) movement at any level, using the same simple principle of guidance - tau-coupling action-gaps. The theory satisfies the general principles of animal movement set out at the beginning of this article, namely that purposeful movement requires prospective control, that the perceptual information guiding movement must extrapolate the movement into the future and be readily available, that movement requires constant intrinsic-cum-perceptual guidance, and that movement guidance must be simple and reliable. The theory is thus biologically plausible. It is formulated mathematically and so can make measurable predictions, which enables it to be tested and developed - and also used to assess skill in guiding movement in a precise quantitative way. The theory is still

evolving and there are a number of problems yet to solve - for example, how to explain the group-guidance of temporally-nested sub-movements that make up concerted acts such as shifting gaze (section 15) running (section 16.2), and playing the piano. Indeed, musical movement, taken to mean not only singing, instrument playing and dancing but also gesturing and vocal articulation - in short, communicative musicality (ref) - comprises a rich source of information about guided movement and fertile ground for testing and developing the theory. Musical movement also potentially provides unique insight into the workings of the nervous system, since that is where the extrinsic patterns of movement originate. There must therefore be patterns of neural activity that correspond to the extrinsic movements. If the patterns of musical movements can be accurately described in term of general tau theory, as we have evidence that they can (section 17), then those same patterns can be sought in the brain, as we are currently doing (section 19).

If general tau theory applies to guiding the body through the environment then it might be expected to apply also to the movements within the body that support, and need to be synchronized with, bodily movement. The movements associated with respiration and pumping blood around the body are obvious cases. Though these are traditionally considered autonomic movements, breathing clearly can be under purposive prospective control, as when speaking or singing, and the pumping of the heart may well be too, as our studies of the build-up of heart-rate prior to strenuous activity would indicate. My colleagues and I are currently applying general tau theory to try to gain a more precise understanding of the pumping action of the heart.

There are a myriad of other movements within the body that are necessary for sustaining bodily movement, including the army of cells in the immune system and the very much vaster number of beneficial bacteria that play a crucial role in the life of an organism. Microbes move themselves around using sophisticated means of propulsion and are sensitive to an impressive number of patterns of energy, including light, gravity, chemical concentration, vibration and electromagnetic fields. The traditional view is that they simply *react* to changes in the energy fields. However, given the sophistication of their sensory and motor systems, which in many ways match those of larger organisms, and given the evolutionary success of microbes such as bacteria, which leaves all larger

animals far behind, it seems not unlikely that they have evolved means of prospectively guiding their movements. Whether or not this involves tau is a question we are currently pursuing, using paramecia and *C. elegans* initially to show us the way. It has, of course, not escaped our notice that there are potential medical applications of this line of enquiry: the more we can learn about how microbes guide their movements using sensory information the better able will we be to create sensory informational fields to steer pathogens away from places where they do harm.

I conclude with another potential medical application of general tau theory - the diagnosis and treatment of infants with neuro-developmental disorders. Babies born very prematurely and/or with low birthweight are considered to be neurologically at risk. However, it is often difficult to diagnose precisely what, if anything, is neurologically wrong. If diagnosis could be improved then so could therapy. General tau theory offers help in that it provides a way of precisely measuring movement guidance in young babies. For example, nutritive sucking and gesturing with the arms and legs are two tauG guided skills that develop early in healthy infants (section 14). Therefore they could be used as benchmarks for assessing neurologically at-risk babies. We need more measures of the tauG guidance capabilities of healthy infants to build up a battery of benchmarks. These could then be applied in the neurological assessment of at-risk babies, and in the design and evaluation of remedial therapies. The need is increasingly urgent as more and more babies are successfully delivered prematurely as a result of improvement in perinatal care.

Readers who are inspired to join the quest for solving the problems I have outlined in this paper, or related problems, may wish first to visit our website (<http://www.perception-in-action.ed.ac.uk>) before contacting me directly.

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## APPENDIX

### A1 Derivation of the specifying equations resulting from linear movement of the point(s) of observation (figure 4)

First a word needs to be said about the importance of establishing a perceptual frame of reference for guiding movement. Any measurement has to be made with respect to an appropriate frame of reference. When guiding locomotion by vision or echolocation, for example, the perceptual frame of reference within which the optical or acoustic flow is measured has to be fixed to the point(s) of observation and be non-rotating relative to the instantaneous direction of motion and a fixed direction in the environment, such as gravity. I shall refer to this frame of reference as the locomotor frame. If perceptual measurements were not made in the locomotor frame (or in a frame moving in a known way with respect to it) then the sensed directions of objects would alter in an arbitrary way relative to the animal's motion path. Such would happen, for example, if the gaze were fixed on a nearby object to the side and the frame of reference were locked to the retina.

Thus, to guide its movement through the environment, an animal needs to establish a locomotor frame of reference. This requires sensing the instantaneous direction of motion and sensing the direction of gravity - e.g., through the vestibular system and/or vision. Establishing a locomotor frame is an active process, as is indicated by such phenomena as post-rotatory dizziness, where the temporary disturbance to the vestibular system impairs the ability to orient. In what follows it is assumed that the animal sets up a frame of reference that places the optic projection surface(s) perpendicular to the straight ahead, whether the head is moving straight ahead, or sideways or vertically, since this simplifies the sensory specification of an extrinsic action-gap. To set up any other frame of reference would result in more complex sensory specification (see Bootsma & Oudejans, 1993; Tresilian, 1994).

#### A1.1 *Monocular specification of the taus and directions of T and G*

Referring to figure 4b, from similar triangles:

$$X_T/Z_T = x_T/d \quad (14)$$

$$Y_T/Z_T = y_T/d \quad (15)$$

$$X_T/Y_T = x_T/y_T \quad (16)$$

$$X_G/Z_G = x_G/d \quad (17)$$

$$Y_G/Z_G = y_G/d \quad (18)$$

$$X_G/Y_G = x_G/y_G \quad (19)$$

Equations (16) and (19) show that the directions of T and G are optically specified by  $x_T/y_T$  and  $x_G/y_G$  respectively.

(i) For horizontal frontal-plane movement of the point of observation O with velocity  $V_X$ ,  $Y_T$ ,  $Z_T$ ,  $Y_G$ ,  $Z_G$ , and  $d$  are constant and so equations (14) and (17) are power law relations between  $X_T$  and  $X_G$  and optical parameters. Hence, from the power-law/tau-coupling duality (section 10):

$$\tau(X_T) = -X_T/V_X = \tau(x_T) \quad (20)$$

$$\tau(X_G) = -X_G/V_X = \tau(x_G) \quad (21)$$

(ii) For vertical movement of the point of observation O with velocity  $V_Y$ ,  $X_T$ ,  $Z_T$ ,  $X_G$ ,  $Z_G$ , and  $d$  are constant and so equations (15) and (18) are power law relations between  $Y_T$  and  $Y_G$  and optical parameters. Hence, from the power-law/tau-coupling duality (section 10):

$$\tau(Y_T) = -Y_T/V_Y = \tau(y_T) \quad (22)$$

$$\tau(Y_G) = -Y_G/V_Y = \tau(y_G) \quad (23)$$

(iii) For forward linear movement of the point of observation O with velocity  $V_Z$ ,  $X_T$ ,  $Y_T$ ,  $X_G$ ,  $Y_G$ ,  $x_G$ ,  $d$  are constant and so equations (14), (15), (18) are power law relations between  $Z_T$  and  $Z_G$  and optical parameters. Hence, from the power-law/tau-coupling duality (section 10):

$$\tau(Z_T) = -Z_T/V_Z = -\tau(x_T) \quad (24)$$

$$\tau(Z_T) = -Z_T/V_Z = -\tau(y_T) \quad (25)$$

$$\tau(Z_T) = -Z_T/V_Z = -\tau(r_T) \quad (26)$$

$$\tau(Z_G) = -Z_G/V_Z = -\tau(y_G) \quad (27)$$

(The proof of equation (26) is as follows. From Pythagoras,  $r_T^2 = x_T^2 + y_T^2$ , hence, differentiating with respect to time,  $r_T \dot{r}_T = x_T \dot{x}_T + y_T \dot{y}_T$ . This equation can be written as:

$$\tau(r_T) \dot{r}_T^2 = \tau(x_T) \dot{x}_T^2 + \tau(y_T) \dot{y}_T^2. \text{ But } \dot{r}_T^2 = \dot{x}_T^2 + \dot{y}_T^2 \text{ and, from equations (24) and (25),}$$

$$\tau(y_T) = \tau(x_T). \text{ Therefore, } \tau(r_T) = \tau(x_T) = \tau(y_T).$$

#### A1.2 Binocular specification of the taus of $T$

Referring to figure 4b, from similar triangles:

$$x_L = -d(X_T - a)/Z_T \quad (28)$$

$$x_R = -d(X_T + a)/Z_T \quad (29)$$

$$y_L = dY_T/Z_T \quad (30)$$

$$y_R = dY_T/Z_T \quad (31)$$

and from equations (28) and (29):

$$x_L + x_R = -2dX_T/Z_T \quad (32)$$

$$x_L - x_R = 2ad/Z_T \quad (33)$$

(i) For horizontal frontal-plane movement of the points of observation  $O_L$  and  $O_R$ ,  $Z_T$  is constant and so applying the power-law/tau-coupling duality (section 10) to equation (32):

$$\tau(X_T) = \tau(x_L + x_R) \quad (34)$$

(ii) For vertical movement of the points of observation  $O_L$  and  $O_R$ ,  $Z_T$  is constant and so applying the power-law/tau-coupling duality to equations (30) and (31):

$$\tau(Y_T) = \tau(y_L + y_R) \quad (35)$$

(iii) For forward linear movement of the points of observation  $O_L$  and  $O_R$ ,  $X_T$  and  $Y_T$  are constant and so applying the power-law/tau-coupling duality to equations (28) to (33):

$$\begin{aligned} \tau(Z_T) &= -\tau(x_L) = -\tau(x_R) = -\tau(y_L) = -\tau(y_R) \\ &= -\tau(y_L + y_R) = -\tau(x_L + x_R) = -\tau(x_L - x_R) \end{aligned} \quad (36)$$

*A1.3 Monocular specification of the spatial coordinates ( $X_T$ ,  $Y_T$ ,  $Z_T$ ) of  $T$  in terms of tau, direction and eye height  $Y_G$*

(i) For horizontal frontal-plane movement of the point of observation  $O$  with velocity  $V_X$ , eliminating  $V_X$  between equations (20) and (21):

$$X_T/X_G = \tau(x_T)/\tau(x_G) \quad (37)$$

Eliminating  $X_G$  between equations (19) and (37):

$$X_T/Y_G = (x_G/y_G)(\tau(x_T)/\tau(x_G)) \quad (38)$$

Eliminating  $X_T$  between equations (16) and (38):

$$Y_T/Y_G = (y_T/x_T)(x_G/y_G)(\tau(x_T)/\tau(x_G)) \quad (39)$$

Eliminating  $X_T$  between equations (14) and (38):

$$Z_T/Y_G = -(d/x_T)(x_G/y_G)(\tau(x_T)/\tau(x_G)) \quad (40)$$

$(x_G/y_G)$ ,  $(y_T/x_T)$  and  $(d/x_T)$  are the *directional terms* in the specifying equations (38), (39) and (40).

(ii) For vertical movement of the point of observation O the eye-height  $Y_G$  changes and so cannot be used as a scaling factor.

(iii) For forward linear movement of the point of observation O with velocity  $V_Z$ , eliminating  $V_Z$  between equations (25) and (27):

$$Z_T/Z_G = \tau(y_T)/\tau(y_G) \quad (41)$$

Eliminating  $Z_G$  between equations (18) and (41):

$$Z_T/Y_G = (d/y_G)(\tau(y_T)/\tau(y_G)) \quad (42)$$

Eliminating  $Z_T$  between equations (15) and (42):

$$Y_T/Y_G = (y_T/y_G)(\tau(y_T)/\tau(y_G)) \quad (43)$$

Eliminating  $Y_T$  between equations (16) and (43):

$$X_T/Y_G = (x_T/y_G)(\tau(y_T)/\tau(y_G)) \quad (44)$$

*A1.4 Monocular specification of the velocity and acceleration of the point of observation in terms of tau, direction and eye height  $Y_G$*

(i) For horizontal frontal-plane movement of the point of observation O with velocity  $V_X$  and acceleration  $A_X$ , eliminating  $X_G$  between equations (19) and (21):

$$V_X/Y_G = -(x_G/y_G)(1/\tau(x_G)) \quad (45)$$

Differentiating equation (45) with respect to time:

$$A_X/Y_G = -(x_G/y_G)(1 - \dot{\tau}(x_G))/\tau^2(x_G) \quad (46)$$

(ii) For vertical movement of the point of observation O the eye-height  $Y_G$  changes and so cannot be used as a scaling factor.

(iii) For forward linear movement of the point of observation O with velocity  $V_Z$  and acceleration  $A_Z$ , eliminating  $Z_G$  between equations (18) and (27):

$$V_Z/Y_G = (d/y_G)(1/\tau(y_G)) \quad (47)$$

Differentiating equation (47) with respect to time:

$$A_Z/Y_G = (d/y_G)(1 + \dot{\tau}(y_G))/\tau^2(y_G) \quad (48)$$

*A1.5 Monocular specification of the spatial coordinates ( $X_T$ ,  $Y_T$ ,  $Z_T$ ) of T by tau and direction in locomotor units*

Referring to figure 4a,b, suppose the person is running at a constant speed. Let the duration of a step be  $t_s$  and the length of a step be one locomotor unit. Then, *measuring in locomotor units*, from equations (14), (15), (24), (25) and (26):

$$X_T = -(x_T/d)\tau(x_T)/t_s = -(x_T/d)\tau(y_T)/t_s = -(x_T/d)\tau(r_T)/t_s \quad (49)$$

$$X_T = -(y_T/d)\tau(x_T)/t_s = -(y_T/d)\tau(y_T)/t_s = -(y_T/d)\tau(r_T)/t_s \quad (50)$$

$$Z_T = -\tau(x_T)/t_s = -\tau(y_T)/t_s = -\tau(r_T)/t_s \quad (51)$$

where  $(x_T/d)$  and  $(y_T/d)$  are the directional terms.

*A1.6 Monocular specification of the spatial coordinates ( $X_T$ ,  $Y_T$ ,  $Z_T$ ) of  $T$  in terms of tau and direction and the velocity or acceleration of the point of observation*

(i) For horizontal frontal-plane movement of the point of observation O with velocity  $V_X$  and acceleration  $A_X$ , from equation (20):

$$X_T/V_X = -\tau(x_T) \quad (52)$$

Eliminating  $X_T$  between equations (16) and (51), and between (14) and (51):

$$Y_T/V_X = -(y_T/x_T)\tau(x_T) \quad (53)$$

$$Z_T/V_X = -(d/x_T)\tau(x_T) \quad (54)$$

Differentiating equations (52), (53) and (54) with respect to time:

$$X_T/A_X = \tau^2(x_T)/(\dot{\tau}(x_T) - 1) \quad (55)$$

$$Y_T/A_X = (y_T/x_T)\tau^2(x_T)/(\dot{\tau}(x_T) - 1) \quad (56)$$

$$Z_T/A_X = (d/x_T)\tau^2(x_T)/(\dot{\tau}(x_T) - 1)) \quad (57)$$

(ii) For vertical movement of the point of observation O with velocity  $V_Y$  and acceleration  $A_Y$ , from equation (22):

$$Y_T/V_Y = -\tau(y_T) \quad (58)$$

Eliminating  $Y_T$  between equations (16) and (58), and between (15) and (58):

$$X_T/V_Y = -(x_T/y_T)\tau(y_T) \quad (59)$$

$$Z_T/V_Y = -(d/y_T)\tau(y_T) \quad (60)$$

Differentiating equations (59), (58) and (60) with respect to time:

$$X_T/A_Y = (x_T/y_T)\tau^2(y_T)/(\dot{\tau}(y_T) - 1)) \quad (61)$$

$$Y_T/A_Y = \tau^2(y_T)/(\dot{\tau}(y_T) - 1)) \quad (62)$$

$$Z_T/A_Y = (d/y_T)\tau^2(y_T)/(\dot{\tau}(y_T) - 1)) \quad (63)$$

(iii) For forward linear movement of the point of observation O with velocity  $V_Z$  and acceleration  $A_Z$ , from equations (24) and (25):

$$Z_T/V_Z = \tau(x_T) \quad (64)$$

$$Z_T/V_Z = \tau(y_T) \quad (65)$$

Eliminating  $Z_T$  between equations (14) and (64), (14) and (65), (15) and 63), (15) and (61):

$$X_T/V_Z = (x_T/d)\tau(x_T) \quad (66)$$

$$X_T/V_Z = (x_T/d)\tau(y_T) \quad (67)$$

$$Y_T/V_Z = (y_T/d)\tau(x_T) \quad (68)$$

$$Y_T/V_Z = (y_T/d)\tau(y_T) \quad (69)$$

Differentiating equations (66), (67), (68), (68), (64), (65) with respect to time:

$$X_T/A_Z = -(x_T/d)\tau^2(x_T)/(1 + \dot{\tau}(x_T)) \quad (70)$$

$$X_T/A_Z = -(x_T/d)\tau^2(y_T)/(1 + \dot{\tau}(y_T)) \quad (71)$$

$$Y_T/A_Z = -(y_T/d)\tau^2(x_T)/(1 + \dot{\tau}(x_T)) \quad (72)$$

$$Y_T/A_Z = -(y_T/d)\tau^2(y_T)/(1 + \dot{\tau}(y_T)) \quad (73)$$

$$Z_T/A_Z = \tau^2(x_T)/(1 - \dot{\tau}(x_T)) \quad (74)$$

$$Z_T/A_Z = \tau^2(y_T)/(1 - \dot{\tau}(y_T)) \quad (75)$$

### Figure captions

**Figure 1.** Keeping tau-dot of an action-gap (m-g) constant to control deceleration: (a) stopping a vehicle at an obstacle, (b) humming bird docking on a feeder tube, (c) pigeon landing on a perch, (d) controlling angular deceleration to land upright from a somersault, (e) bat slowing down to fly through a hole, (f) bat landing on a perch. Section (4) for details.

**Figure 2.** Fitting actions into time-slots: (a) Diving gannet, (b) leaping to punch a falling ball, (c) ski-jumping, (d) long jumping, (e) running on 'stepping-stones'. (f) crossing a pretend road. Section (6) for details.

**Figure 3.** Tau-coupling action-gaps: (a) bat landing on a perch (action-gaps X and A were tau-coupled), (b) raising food to the mouth ( $\tau_\alpha$  and  $\tau_r$  were coupled), (c) child hitting a hanging bat with the hand to strike an approaching ball (the hand/bat and ball/bat action-gaps were tau-coupled), (d) interception task where an adult moved the hand cursor, H, vertically up the computer screen so that it stopped in the goal zone, G, just as the target cursor, T, which moved in a straight line from the bottom left or bottom right of the screen with unpredictable constant acceleration, deceleration or speed, reached the goal zone (action-gaps HT and HG were tau-coupled). Section (8) for details.

**Figure 4.** Optic flow-field(s) resulting from linear movement. (a) Forward linear movement of the point of observation O produces an optic flow-field consisting of an expanding bundle of narrow optic cones with their apices at O and their bases on surface texture elements in the environment. (b) Notation for describing the monocular optic flow-field. A model projection plane perpendicular to the OZ axis is at a fixed distance, d, behind O. The projection plane and the rectangular Cartesian coordinate frame OXYZ move together. The points T\* and G\* on the projection plane are the images of the points T and G from the tree and ground as projected through O. The coordinates of the points with respect to the moving coordinate frame OXYZ are as shown. Lowercase letters designate optical quantities, uppercase letters designate physical quantities. The optic flow-field is characterized by the changing coordinates of the points on the projection

plane when O moves. The information afforded by the optic flow-field is described in sections (10.1) and (A1.1). (c) Notation for describing the binocular optic flow-fields. This is similar to the monocular case except that the OXYZ frame is midway between the eyes, and each eye has its own projection plane and point of projection ( $O_L^*$  and  $O_R^*$ ). The information afforded by the binocular optic flow-fields is described in sections (10.2) and (A1.2).

**Figure 5.** Visual guidance of steering. (a) Linear and curvilinear optic flow fields when driving down a road. Section (12.1) for details. (b) Tau information on circular courses. Section (12.2) for details. (c) Steering around and into a bend. Section (12.3) for details. (d) Asymptoting on a surface. Section (12.4) for details. (e) Steering to a goal. Section (12.5) for details.

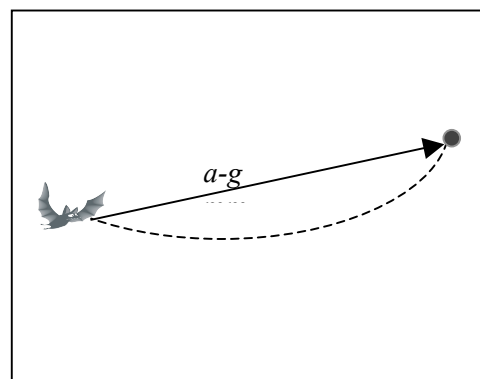
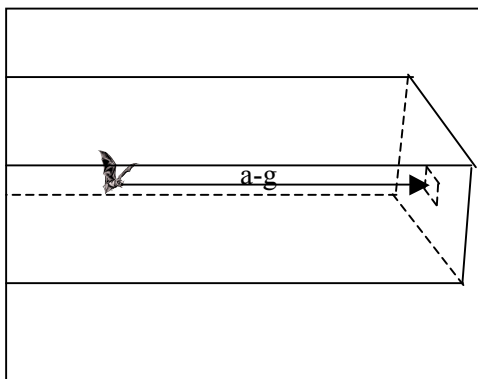
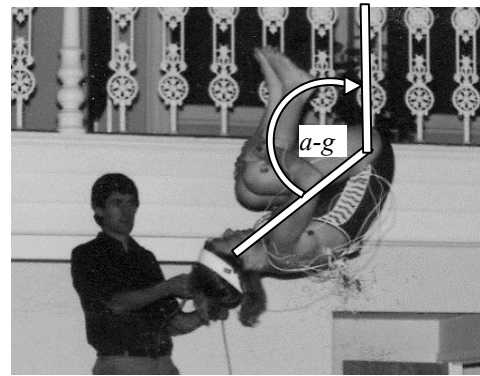
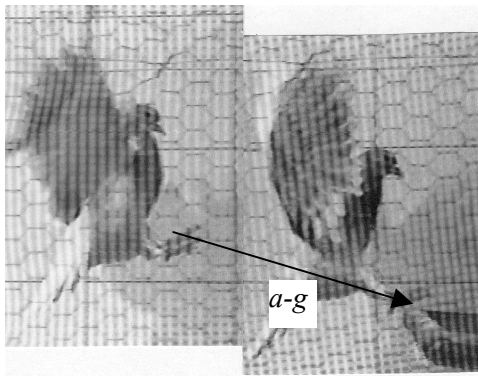
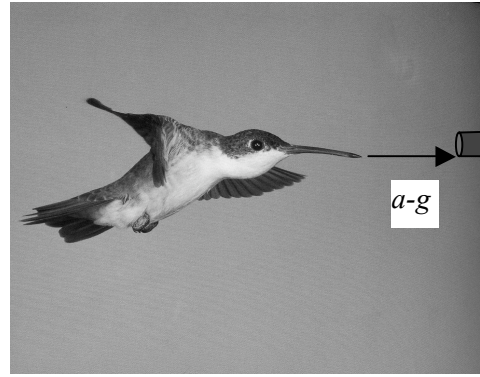
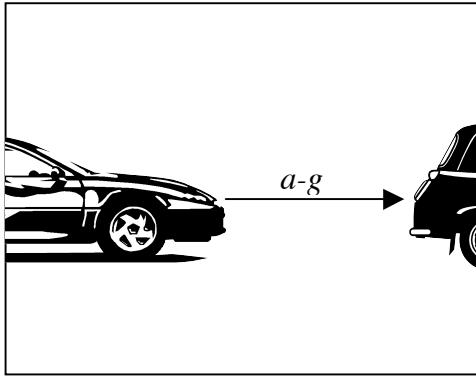
**Figure 6.** Intrinsic guidance of movement by tauG and tauD. (a) How the functions tauG and tauD can be generated by up and down movement of a ball under the constant acceleration of gravity. TauG equals the tau of the vertical action-gap between the ball and the ground. TauD equals the tau of the vertical action-gap between the ball and the zenith. The coloured arcs are to indicate that, ex hypothesis, the tauG or tauD guidance may correspond to only a segment of the up and down movement. (b) and (d) How the size,  $x$ , and velocity,  $\dot{x}$ , of an extrinsic action-gap change over time as a function of  $k$  when the action-gap is tauG guided by following the equation  $\tau(x) = k\tau_G$ . (c) and (e) The same for tauD guidance. Colour code: red,  $k=0.25$ ; orange,  $k=0.5$ ; green,  $k=0.75$ ; light blue,  $k=1.0$ ; dark blue,  $k=1.25$ . Section (13) for details.

**Figure 7.** TauG guided movements. (a) Newborn baby sucking milk from a bottle. An example of the intra-oral pressure and pressure velocity are graphed. The intra-oral

pressure was tightly tauG guided in full-term babies. Section (14.1) for details. (b) 10 week old infant gesturing with arms and legs to music. The gestural movements were tightly tauG guided. Section (14.2) for details. (c) The evolution of head, eye and gaze angles when an adult turned to look at a moving object. The movement segments between successive zero velocity points, indicated by different colours, were tightly tauG guided. Section (15) for details. (d) When varying the length of a putt, the movement of the club from back to front was tightly tauG guided and the length of the putt was controlled by varying parameters of the tauG guided movement. Section (16.1) for details. (e) and (f) Analysis of the movements of the limbs in sprinting revealed overlapping tauG guided movements. Section (16.2) for details.

**Figure 8.** TauG guidance of movement in musical performance. (a) General hypothesis: expressive tauG guided movements by the player produce corresponding expressive tauG guided sounds to which a dancer can respond with corresponding expressive tauG guided movements. Section (17) for details. (b) When singing a classical piece of music, pitch-slides between successive notes were tightly tauG guided and musical stress was varied by varying the value of  $k$  in the tauG guidance equation. Section (17.1) for details. (c) A jazz singer's pitch-slides and accompanying hand gestures were tightly tauG guided using similar values of  $k$ . A trombonist's movements of the slide and the resulting pitch-slides were tightly tauG guided using similar values of  $k$ . Section (17.1) for details. (d) The movement of the bow on the bass and the resulting intensity-slide during the attack on the note were tightly tauG guided: the mood of the playing was modulated by the value of  $k$ . Section (17.2) for details.

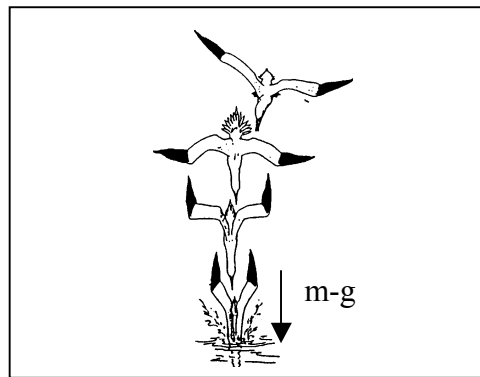
Lee, Figure 1



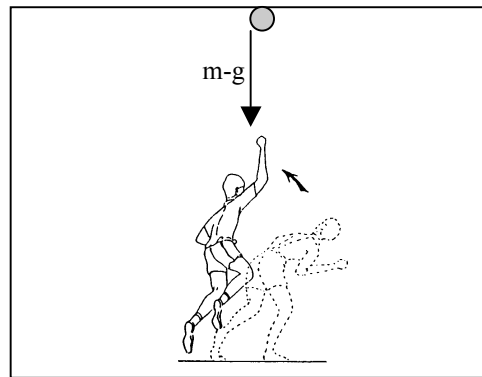
(e)

(f)

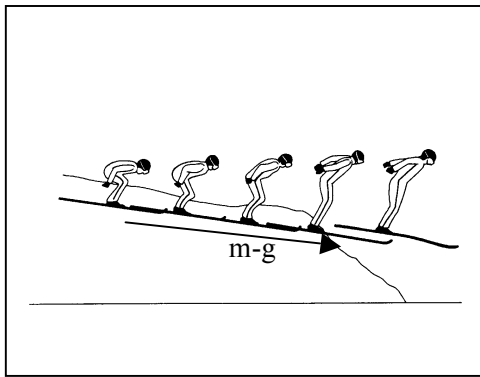
Lee Figure 2



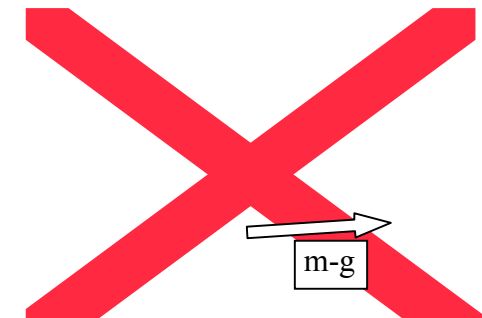
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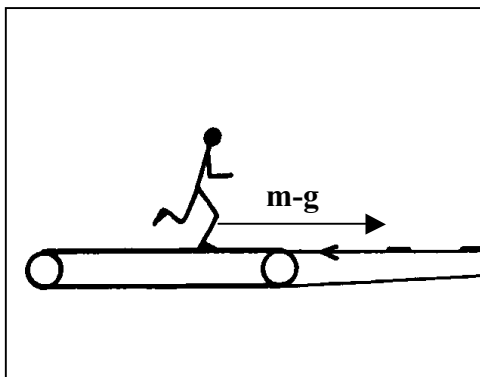
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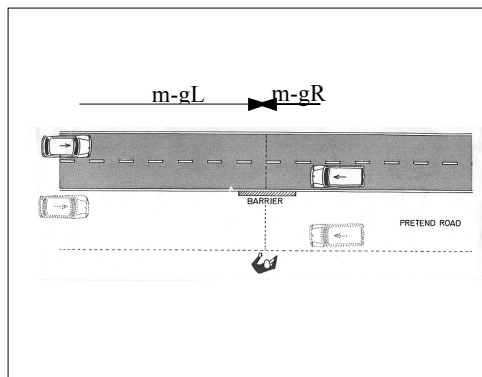
(c)



(d)

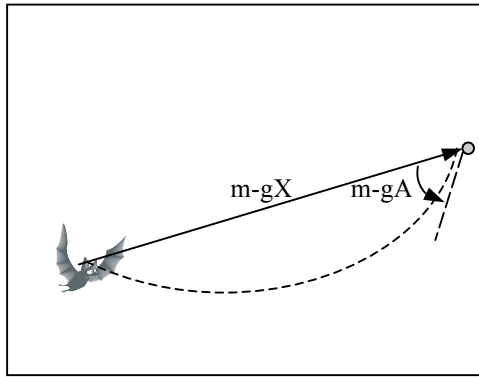


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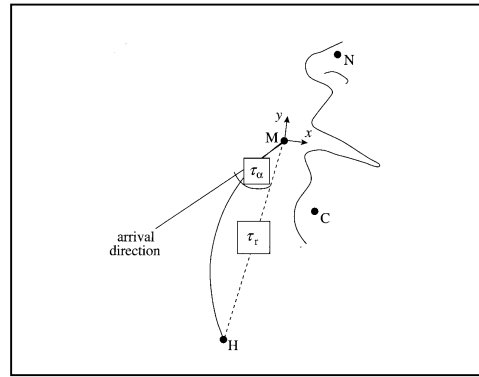


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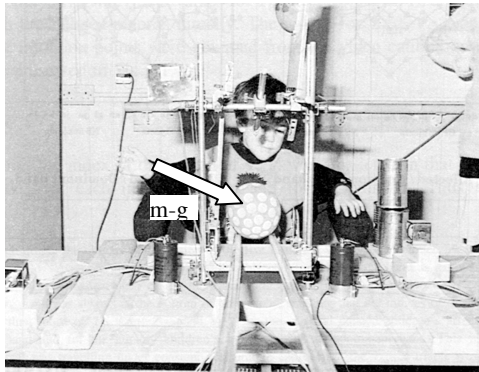
Lee, Figure 3



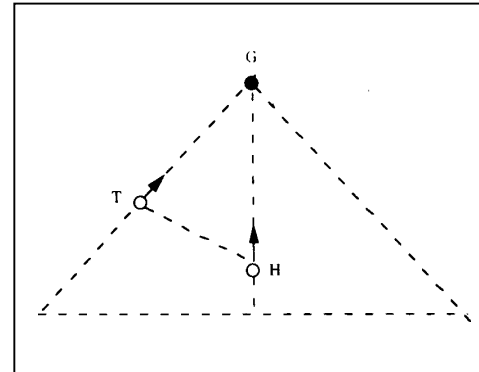
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(b)

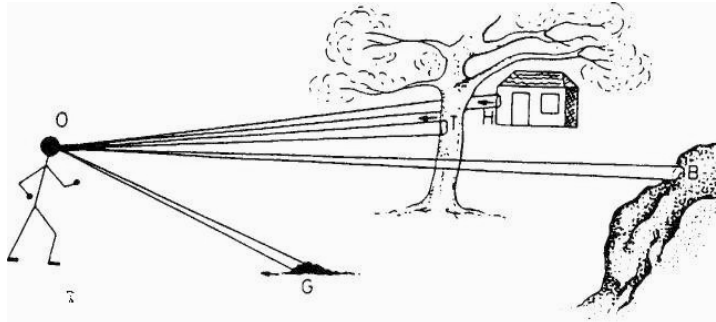


(c)

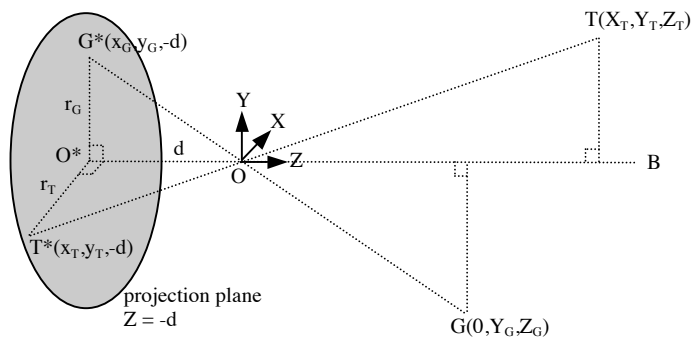


(d)

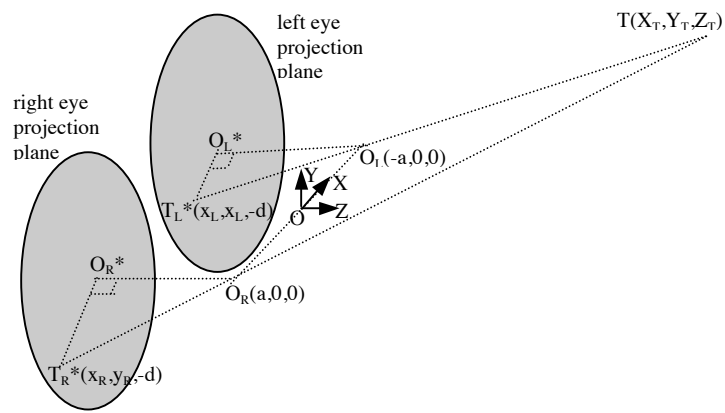
Lee, Figure 4



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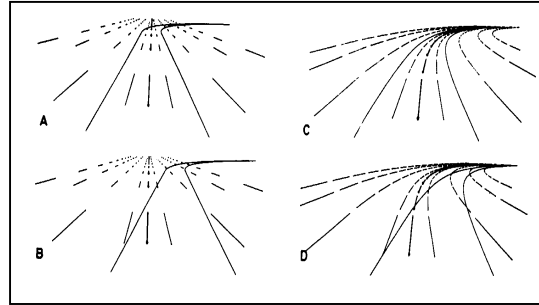


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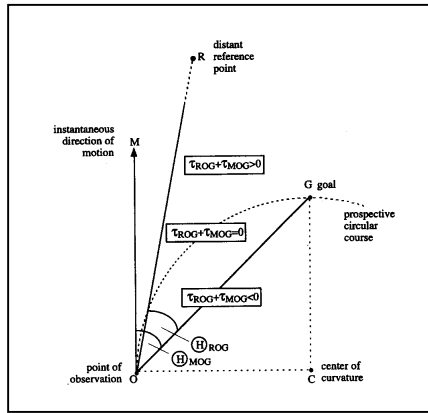


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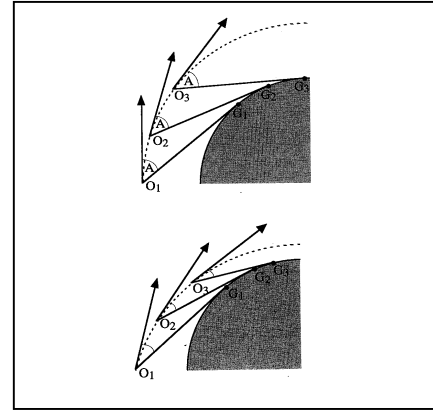
Lee, Figure 5



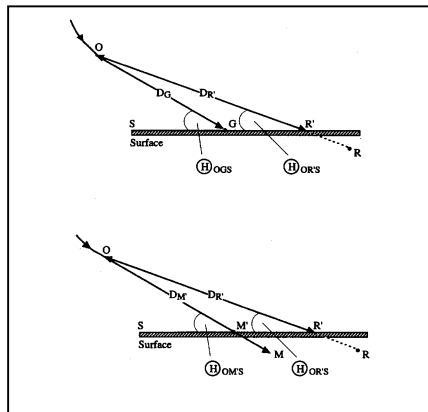
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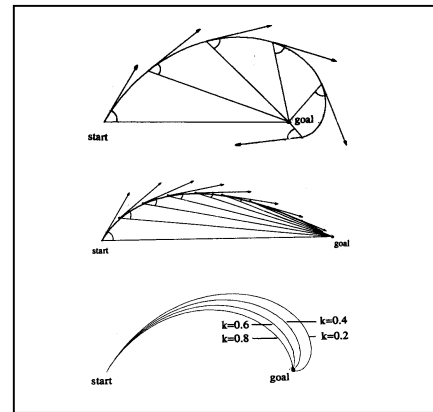
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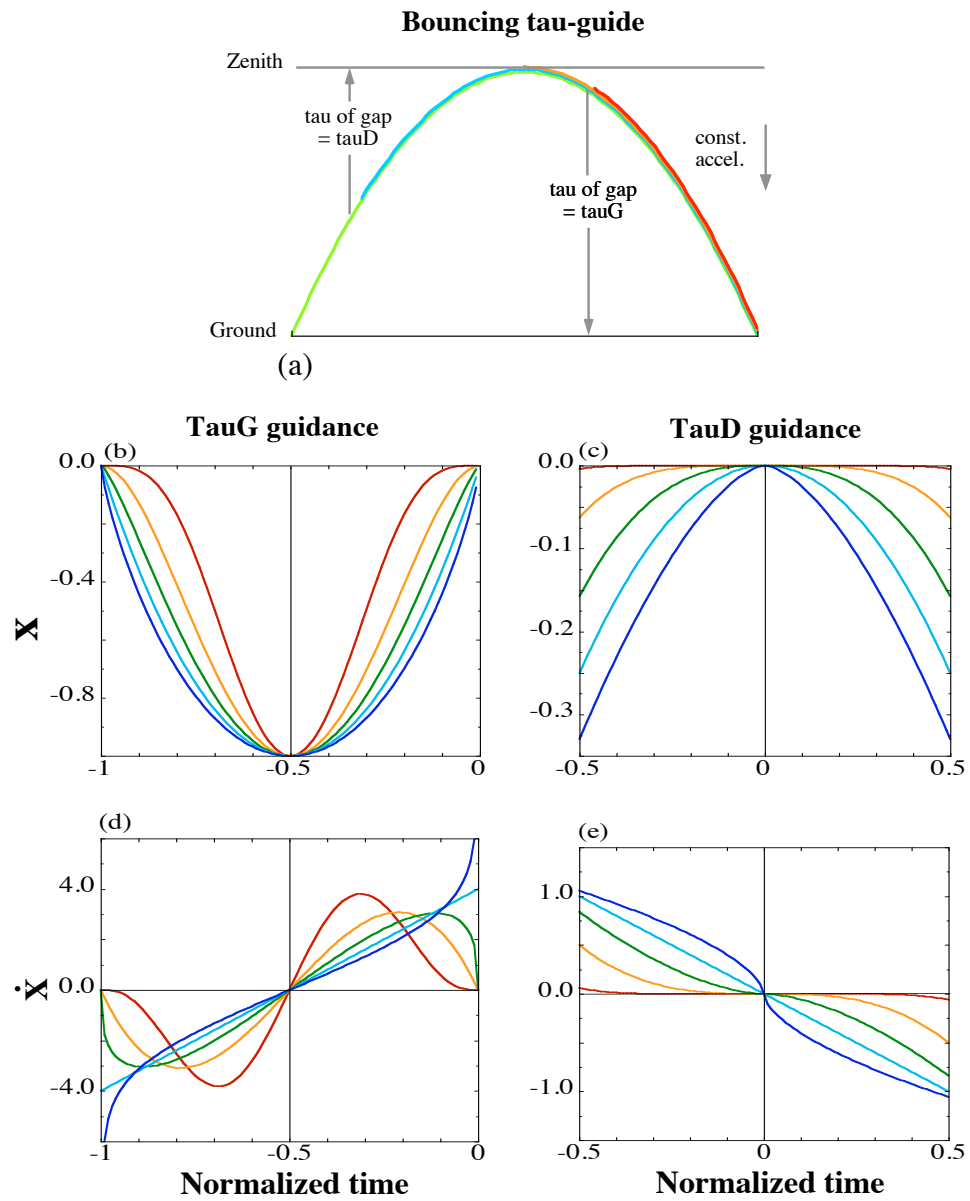


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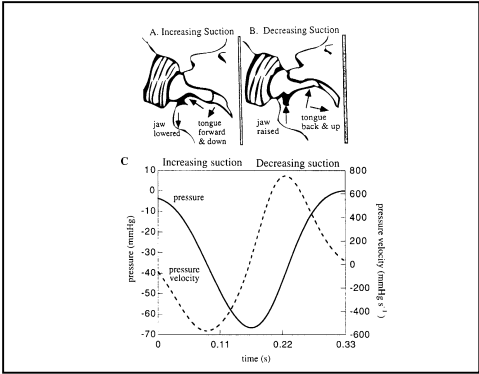


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Lee, Figure 6



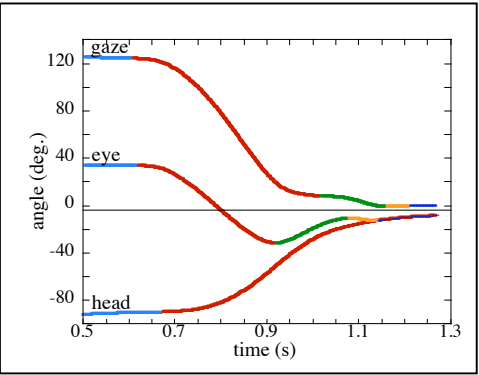
Lee, Figure 7



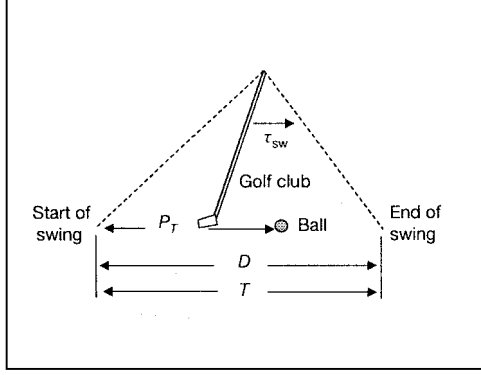
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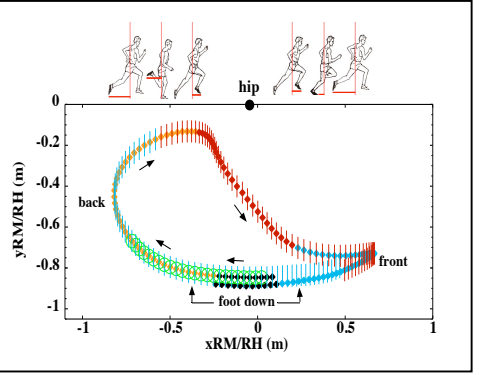
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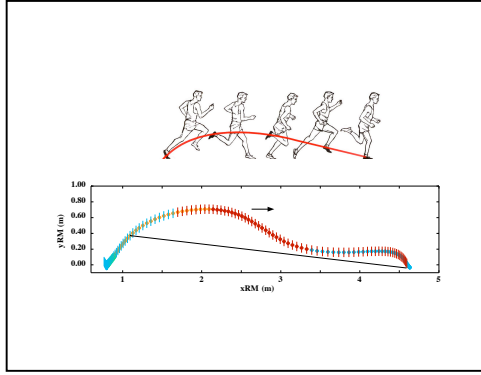
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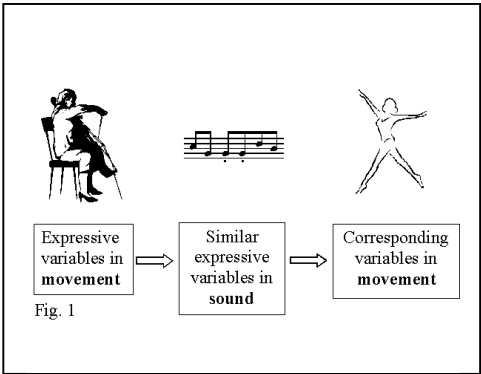
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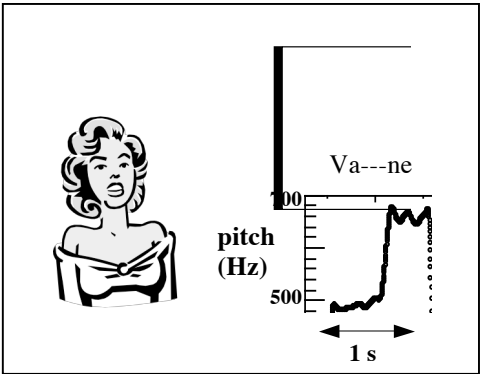
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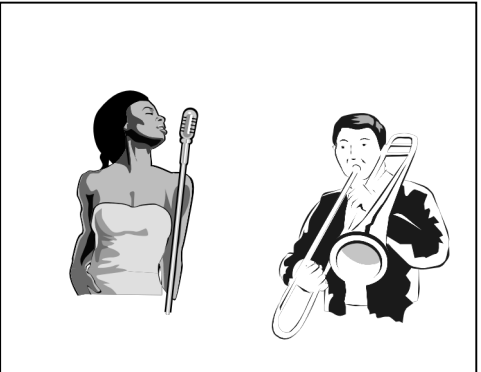
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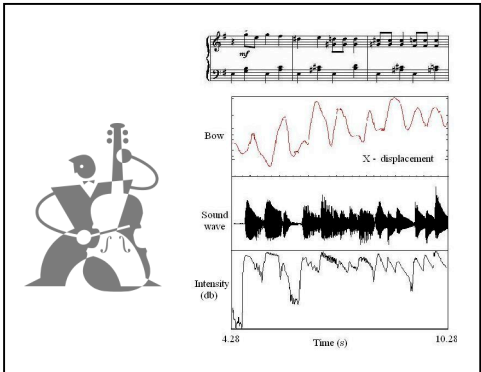
(a)



(b)



(c)



(d)