Guiding Movement by Coupling Taus

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Studies of sensory guidance of movement in animals show that large nervous systems are not necessary for accurate control, suggesting that guidance may be based on some simple principles. In search for those principles, a theory of guidance of movement is described, which has its roots in Gibson's pathfinding work on visual control of locomotion (J. J. Gibson, 1958/this issue). The theory is based on the use of the simple but powerful variable tau, the time-to-closure of a "gap" at the current gap closure rate (whatever the gap's dimension—distance, angle, force, etc.); and on the principle of tau-coupling (keeping two ts in constant ratio). In this article, I show how tau-coupling could be used to synchronize movements and regulate their kinematics. Supportive experimental results are reported. I also show theoretically how sensory-tausts, defined on sensory input arrays, can specify motion-taus through tau-coupling; how the braking procedure of keeping tau-dot stable is a particular case of tau-coupling; and how tools for steering (e.g., limbs, whole bodies, cars, or aircraft) could be built from tau-couplings, which would enable steering control in a variety of situations, including steering straight and curved courses to goals, steering and controlling speed at the same time, steering around obstacles, and asymptoting on surfaces as when landing. Some movements also involve intrinsic guidance from within, and a hypothesis on intrinsic guidance by tau is introduced, supported by experiments spanning different activities.

Animals have to guide their movement through the environment to avoid obstacles, reach destinations safely, intercept moving objects, and so forth. In his seminal article on "Visually Controlled Locomotion and Visual Orientation in Animals," J. J. Gibson (1958/this issue) spelled out the fundamentals of the problem and described some of the basic optical information available for control. His ideas have

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had powerful impact on work in a number of fields in addition to psychology, including neuroscience, neuroethology, computer vision, and robotics.

J. J. Gibson's ideas have also considerably influenced my own thinking, both through his writings and through the many discussions and arguments I had with him, particularly during 1969–1970 when I was working with Jimmy and Jackie Gibson in their perception lab at Cornell. A result of the inspiration I gained during that time was a chapter I wrote for Jimmy's Festschrift (Lee, 1974) on the optic information available during locomotion. There I proposed a hypothesis on how braking (e.g., a car) for an obstacle might be controlled using optic flow variables. The hypothesis was later developed into the theory that braking can be based on information solely about time-to-collision with the obstacle at the current gap closure rate, which is specified by an optic variable that I designated \( \tau \) (Lee, 1976). Since then, \( \tau \) theory has been generalized and tested in various ways. However, those developments are scattered across a number of publications, and they need to be brought together with some new ideas. This celebration of J. J. Gibson's pathfinding article, which was a source of inspiration to me, seems a fitting occasion to summarize the current state of \( \tau \) theory. I would like to dedicate the article to the memory of Jimmy and also to Jackie in enduring gratitude for their inspiration and friendship.

A major concern of general \( \tau \) theory is the use of expropriospecific perceptual information in the guidance of movement in the environment. \( \tau \) theory is about the control of movement via the perception of affordances (E. J. Gibson, 1988; J. J. Gibson, 1979/1986) in that it tackles the problem of defining the information used by animals in apprehending their potential dynamic fit with the environment. The domain of the theory is thus somewhat different from those of other current theoretical approaches to understanding movement, which are mainly concerned with explaining the dynamics of movement production (without much emphasis on the perceptual processes) in terms of solutions to optimization problems (e.g., Alexander, 1997; Flash & Hogan, 1985), or mathematical models of the physioneural structure of the muscles and joints (Bizzi, Mussa-Ivaldi, & Giszter, 1992; Feldman & Levin, 1995) and the abstract underlying dynamics (Beek, Peper, & Stegeman, 1995; Kelso, 1995; Schmidt & Turvey, 1994). These are all important problems but I do not address them in this article. The theoretical links between these approaches and between them and \( \tau \) theory need to be properly explored, but space does not allow me to do that here.

Nor shall I dwell on the problem of determining the sensory information used to initiate movements. This article will concentrate on the guidance of ongoing movements. The movement initiation problem is a tricky one. Several studies indicate that \( \tau \) of the gap between an effector and an object or surface may govern timing of initiation of movement (e.g., Kaiser & Mowafy, 1993; Lee & Reddish, 1981; van der Meer, van der Weel, & Lee, 1994), of neural activity (Wang & Frost, 1992), or discrimination of time of arrival (Regan & Hamstra, 1993). Wann (1996) argued against the strength of some results on movement initiation timing.
(but see also replies to Wann by Bootsma, Fayt, Zaal, & Lautent, 1997, and Tresilian, 1997). There is a problem in doing research on the timing of initiation of interceptive movements that needs to be taken into account in future work. The problem is that it is frequently not critical when a movement starts—just so long as it does not start too late. For example, an experienced driver who knows the car and road conditions can start braking safely for an obstacle a bit later than an inexperienced driver. Thus deciding between competing hypotheses about what perceptual information governs initiation can often be difficult because of the natural variability in the time of initiation. Studying movements that are tightly constrained in start point and duration, like striking movements, could help alleviate that problem.

At the root of general tau theory is the idea of prospective control (e.g., Lee & Young, 1985; von Hofsten, 1993). The guidance of movement has to be prospective because control actions have to be made ahead in time to allow for such factors as inertia. Even under good conditions, stopping a car at an obstacle from 30 mph requires starting to brake when the time-to-collision, if the brakes were not applied, is no less than about 1.5 sec (depending on the power of the brakes). Predictive sensory information is therefore required for prospective control of braking. In general, the higher the speed of travel, the further ahead in time must the predictive information extend. Steering likewise requires acting ahead in time. Achieving the right steering angle for negotiating a bend takes time and so the steering action has to be initiated before the bend is reached. In general, all purposive movements have to be prospectively guided.

General tau theory offers an account of how such guidance might be achieved. I first summarize the principal ideas of the theory and show how these relate to previous narrower concepts of tau. A key idea is that of tau-coupling. Some applications of this idea to understanding guidance of movement are then described. Finally, considering those aspects of skill that require intrinsic timing, as clearly exemplified in musical performance, a hypothesis on intrinsic processes of guidance is introduced.

ELEMENTS OF GENERAL TAU THEORY AS APPLIED TO GUIDING MOVEMENT

General tau theory is not restricted to guidance of movement, but I confine discussion of the theory to that topic in this article. Principal tenets of general tau theory for guiding movement are:

1. A central task in guiding movement is controlling the closure of spatial and/or force gaps between effectors (or sensory organs) and their goals.
2. This requires sensing the closure of gaps in sensory input arrays, for example, optical (vision), acoustic (echolocating bats), force (haptics), electrical
(electrolocating fish and platypus), and electromagnetic (infrared detection by snakes).

3. The tau of each spatial and/or force gap—the time-to-closure of the gap at its current closure rate—is basically what is sensed and controlled constantly to guide the movement.

4. A principal method of movement guidance is by tau-coupling the taus of different gaps, that is, keeping the taus in constant ratio.

Controlling Closure of Gaps

Moving requires guiding limbs and sensory organs to spatial goal positions and angular orientations, and building up forces applied by the body to appropriate goal levels. This all requires perceptual information about how these spatial and force gaps are changing. Often, approaches to several goals have to be rapidly coordinated. Thus, when walking over uneven ground, gaze is shifted from one future footing to the next, and this is accompanied by controlled movement of the feet to those places and careful regulation of the thrust applied to the ground to an appropriate level to propel the body to the next footing.

It might seem reasonable to assume that the body achieves this by sensing gaps in classical Newtonian variables: the angular gap between gaze and the next footing, the distance gap between the foot and the footing, and the force gap between thrust force and goal force. However, angle, distance, and force measures by themselves would not be adequate for controlling approach, because they do not describe how these gaps are changing, so the body would then have to differentiate these gaps with respect to time (as per classical kinematic analysis) to provide first-order, second-order, and perhaps further orders of time differentials (e.g., velocity, acceleration, etc., for the distance gap). However, although this approach represents the standard paradigm we have been taught at school (so that we may perhaps be forgiven for trying to foist this on our bodies), such complex information is unnecessary. There is a single measure on the angle, distance, and force gaps that is sufficient for controlling closure of the gaps, and the body might sense this directly, without recourse to the actual values of angle, distance, and force. That measure is the tau of each gap ($\tau$).

Universal Gap-Measure Tau

Tau of a gap is the time it would take the gap to close at the current closing rate. Tau is taken to be negative when the gap is closing, and positive when it is opening (in which case $\tau$ is the time, at current opening rate, from when the gap was closed). Tau of gap $X$ is also referred to as the tau-function of $X$ (Lee, Reddish, & Rand, 1991). It is symbolized as $\tau_X$ or $\tau(X)$.

Tau is a way of measuring any gap. There is, for example, a $\tau_\Theta$ of the angular gap $\Theta$ between gaze and footing, a $\tau_D$ of the distance gap $D$ between foot and footing,
and a $\tau_F$ of the force gap $F$ between thrust force and goal force. There are also taus of sensory gaps (gaps defined on sensory arrays), which I discuss later. In short, tau is a “formless invariant” (J. J. Gibson, 1979/1986).

Though tau of gap $X$ may be expressed as the ratio $X/\dot{X}$, perceptual systems do not have to register $X$ and $\dot{X}$ to register $\tau_X$. $\tau_X$ could be registered directly. As a related example, though the acceleration of a distance or angular gap $X$ can be expressed as its second temporal derivative, $\ddot{X}$, the vestibular system can register $\dot{X}$ directly without registering $X$. There is evidence suggesting that the eye can indeed register $\tau_X$ directly without registering $X$ or $\dot{X}$ (e.g., Kaiser & Mowafy, 1993; Kim, Turvey, & Carello, 1993; Regan & Hamstra, 1993; Wang & Frost, 1992), but the details need further investigation. Suffice it to say that to find that such systems have indeed evolved would be in accord with general tau theory.

**Tau-Coupling**

Gaps often need to be closed synchronously. For example, when playing a chord on a piano, the fingers have to contact the keys at the same time. A straightforward way of coordinating the closure of two gaps, $X$ and $Y$, is by tau-coupling $\tau_Y$ and $\tau_X$ during the movement; that is, keeping

$$\tau_Y = k\tau_X$$

where $k$ is a constant (see Appendix A). The reason is that, as gap $X$ closes, $\tau_X$ becomes zero. Therefore, if Equation 1 holds, $\tau_Y$ becomes zero at the same time. Thus gap $Y$ closes synchronously with gap $X$.

It can also be shown (see Appendix A) that, if $0 < k < 0.5$ the closure rate of gap $Y$ will get steadily lower at a decreasing rate, and will reach zero as the gap closes (i.e., touch contact). On the other hand, if $0.5 < k < 1$, the closure rate of $Y$ will again get steadily lower but now at an increasing rate until that rate reaches a maximum, with the result that the final closure rate will be positive as the gap closes (i.e., hard contact). In general, the higher the value of $k$ greater than 0.5, the steeper the decrease in closure rate and the higher the closure rate at contact. Thus the parameter $k$ regulates the kinematics of closure of the gap.

Many actions require simultaneously controlling spatial gaps. Controlling direction and speed of approach by synchronizing closure of an angular gap $A$ and a distance gap $X$ is achievable by keeping $\tau_A = k\tau_X$ for constant $k$. For example, echolocating bats swooping in to land on a perch (Lee, Simmons, Saillant, & Buffard, 1995; see Figure 1a) and humans raising food in an arc to the mouth (Lee, Craig, & Grealy, 1998) showed this type of tau-coupling. In another experiment (Lee, Georgopoulos, Clarke, Craig, & Port, 1998), human participants moved, by hand, a cursor on a computer screen to catch a moving target as it reached a goal zone. The results indicated that participants tau-coupled two distance gaps, keeping $\tau_{HG} = k\tau_{HT}$, where $HG =$ hand–goal gap and $HT =$ hand–target gap (Figure 1b).
FIGURE 1  Experimental demonstrations of tau-couplings (indicated by zigzag lines). (a) Echolocating bat flying to a perch. Analysis of flight paths indicated that the bat simultaneously controlled its speed to stop at the perch and its steering to approach the perch from an appropriate direction by tau-coupling $\tau_A$ and $\tau_X$, while keeping $\tau_X$ constant. ($\tau_X$ and $\tau_A$ are the times-to-closure at current closure rate of, respectively, the distance gap $X$ between bat and perch and the angular gap $A$ between the direction from bat to perch and the goal arrival direction.) (b) Target interception experiment on a computer screen (Lee, Georgopoulos, Clark, Craig, & Port, 1998). The target $T$ moved at various constant accelerations, decelerations, or velocities toward the goal and the human participant had to move the hand cursor $H$ so that it stopped at the goal $G$ as the target arrived there. The results indicated that participants solved the task by tau-coupling $\tau_{HT}$ and $\tau_{HG}$, that is, keeping $\tau_{HT} = k \tau_{HG}$ for a constant $k$. (The $\tau$s are the times-to-closure at current closure rate of the gaps $HT$ and $HG$.)

Stabilizing $\dot{\tau}_Y$: A Case of Tau-Coupling

The procedure of controlling braking by keeping $\dot{\tau}_Y$ constant (Lee, 1976) was formulated prior to the idea of tau-coupling. However, it turns out that keeping $\dot{\tau}_Y$ constant is but a particular case of tau-coupling, namely the coupling $\tau_Y = k \tau_X$ when gap $X$ is closing at a constant rate. Or, to anticipate later discussion, keeping $\dot{\tau}_Y$ constant is equivalent to tau-coupling $\tau_Y$ onto a "zero-second-order intrinsic $\tau$-guide" (see later section on Intrinsic Tau-Guidance and Appendix B). Thus, the tau-coupling theorem (Appendix A) applies. This means that when braking keeping $\dot{\tau}_Y = k$, the parameter $k$ regulates the kinematics of closure of the gap to the obstacle in the same way as described in the preceding section (which agrees with the original pre-$\tau$-coupling description: Lee, 1976; Lee, Young & Rewt, 1992).

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1The proof is straightforward. If the closure rate of $X$ is constant then $\dot{\tau}_X = 1$ and so differentiating $\tau_Y = k \tau_X$ with respect to time and substituting $\dot{\tau}_X = 1$ gives $\dot{\tau}_Y = k$. 
Studies across different species indicate that this particular form of tau-coupling, the $\dot{v} = k$ procedure, is used widely in controlling velocity of approach; for example, by humans landing from somersaults (Lee, Young, & Rewt, 1992) and braking in a driving simulator (Yilmaz & Warren, 1995); by hummingbirds aerially docking on a feeder (Lee et al., 1991) and pigeons landing on a perch (Lee, Davies, Green, & van der Weel, 1993); and by echolocating bats slowing down to fly through a hole (Lee, van der Weel, Hitchcock, Matejowsky, & Pettigrew, 1992) and to land on a perch (Lee et al., 1995).

**Sensory-Tau–Motion-Tau Coupling**

In this section I show how motion-taus are perceptually specifiable by means of tau-couplings to sensory-taus. Motion-taus include spatial-taus and force-taus (just as Newton's Laws of Motion involve both space and force). However, in the following discussion I concentrate on spatial-taus because they are easier to visualize. First a word needs to be said about establishing an expropriospecific frame of reference for guiding movement.

*Motion frame of reference.* Any form of measurement has to be made within an appropriate frame of reference. When guiding movement by vision or echolocation, for example, the frame of reference within which the perceptual system measures the optical or acoustic flow has to be fixed to the point of observation and nonrotating relative to the instantaneous direction of motion and a fixed direction in the environment such as gravity. I refer to this frame of reference as the *motion frame.* (A frame of reference moving in a known way relative to this frame can be treated as equivalent, because there is a specified mapping between the frames.) If perceptual measurements were not made in the motion frame (or equivalent frame, as just defined) 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.

The motion frame of reference is expropriospecific. It is fixed to neither the body nor the environment but encompasses the two. It is a frame in which affordances may be measured. To guide movement an animal needs to establish a motion frame of reference. This essentially requires sensing the instantaneous direction of motion and sensing the direction of gravity; for example, through the vestibular system and/or vision. Establishing a motion frame is an active process, as is indicated by such phenomena as postrotatory dizziness, where the temporary disturbance to the vestibular system impairs the ability to orient.

As J. J. Gibson (1950) pointed out, a straight course generates an optic flow field at the point of observation $O$ that is characterized by a radial outflow of optic elements from a center, which corresponds to the instantaneous direction of motion. Human
observers can perceive direction of locomotion with respect to a goal to an accuracy of about 1°, from the optic flow from a simulated textured ground surface, even when optical rotation simulating eye movement is added to the display (Warren & Hannon, 1988; see also Bradley, Maxwell, Anderson, Banks, & Shenoy, 1996, for neurophysiological evidence). Though the accuracy of such judgments seems to depend on the speed of eye movement (Royden, Banks, & Crowell, 1992), the perceptual system appears robust, being able to tolerate the addition of optical noise to the display (van den Berg, 1992). Thus, it may be concluded that the motion frame of reference can be accurately established visually. There is no reason to doubt that the motion frame can be established nonvisually, too. One can, for example, walk with reasonable accuracy to a sound source with eyes closed—presumably by coupling haptic information through the feet with articular and acoustic-directional information, to sense the direction of the sound relative to the current direction of motion. The ability of echolocating bats to catch insects on the wing (Simmons, Dear, Ferragamo, Haresign, & Fritz, 1996) would clearly indicate that they can accurately establish a motion frame of reference through hearing.

**Sensory specification of motion-taus.** Let us now consider how motion-taus might be specified by means of tau-couplings to sensory-taus. It follows from the tau-coupling theorem (Appendix A), or rather its converse, that if (but only if) a gap, s, within a sensory array is a power function of a motion gap, M (so that \( s = CM^\sigma \) for constants C and \( \sigma \)) then

\[
\tau_M = \sigma \tau_s.
\]  

Thus the motion-tau, \( \tau_M \), is tau-coupled onto the sensory-tau, \( \tau_s \), and its value is therefore directly specified by the value of the sensory-tau (to within a constant scale-factor \( \sigma \)). Hence, in principle, an animal may tau-couple motion-taus by acting in such a way as to tau-couple the corresponding sensory-taus.

We shall now apply the power law criterion (\( s = CM^\sigma \)) to determine sensory-taus (\( \tau_s \)) that could specify motion-taus (\( \tau_M \)) during movement. Figure 2a diagrams a motion frame of reference. The line OZ is the instantaneous direction of motion. Plane OYZ is parallel to gravity. P is a stationary texture element in the environment. Two coordinate systems for measuring the sensory flow are shown—a projection sphere centered on the point of observation O, using spherical polar coordinates (1, θ, φ) and \((R, \Theta, \Phi)\) for the image and object elements respectively; and a frontal projection plane, using rectangular coordinates (x, y, 1) and (x, y, z) for the image and object elements. Figure 2b shows the image on the projection plane of an additional element Q lying on the same frontal plane as P. The sensory gap between the images \( P' \) and \( Q' \) is \( w \).

Some sensory-tau—motion-tau couplings that are available to animals and could be used in guiding movement are listed in Table 1. Whether the couplings are in fact used remains, for the most part, to be determined by experiment. Sensory gaps
FIGURE 2  Notation for describing the sensory flow field at a point of observation O. See text for details.

and taws are symbolized by lower case letters, motion gaps and taws by upper case letters. Except where otherwise noted, the notation follows that in Figure 2. Let us consider the table row by row.

Rows 1 and 2: $w_0$ and $w$ are the sensory image gaps shown in Figure 2b. As regards $w_0$, $C$ in the power law equations is the distance of $P$ from the motion line $OZ$ (Figure 2a). As regards $w$, $C$ is the separation of $P$ and $Q$ (as can be shown by simple geometry). Assuming $C$ is unknown to the animal in either case then neither $w_0$ nor $w$ can specify the motion gap $Z$ via the power law equations. $\tau_2$ is however specified by $\tau_{w_0}$ and $\tau_W$ through the tau-coupling equations.

$\tau_{w_0}$ and $\tau_W$ correspond to the original definition of tau as an optic variable (Lee, 1976, 1980). $\tau_2$ corresponds to the so-called "tau-margin" (Lee & Young, 1986).

That motion-tau ($\tau_2$) can be visually sensed through $\tau_{w_0}$ or $\tau_W$ is indicated by experiments visually simulating approach, including experiments recording from nucleus rotundus in pigeon (Wang & Frost, 1992) and human psychophysical experiments (e.g., Kaiser & Mowafy, 1993; Kim, et al., 1993; Regan & Hamstra, 1993). The idea needs to be tested on echolocation.

Row 3: $\omega$, in Figure 2b, is now treated as the sensory gap corresponding to the motion gap $W$ between two points on a frontal plane; for example, between a laser pointer and the point on the screen to which it is being moved. We assume the animal sets up a frame of reference that places the motion in a frontal plane, because this makes the sensory specification of the motion-tau, $\tau_W$, simple and direct by the tau-coupling $\tau_W = \tau_{w}$. (The motion distance, $W$, is, however, not specified unless the distance to the screen—$1/C$ in the power law equation—is known.) To set up
### TABLE 1
Sensory-Tau-Motion-Tau Couplings Resulting From Power Law Relations Between Sensory Gaps and Motion Gaps

<table>
<thead>
<tr>
<th>Row</th>
<th>Perceptual System</th>
<th>Sensory Gap</th>
<th>Dimension</th>
<th>Motion Gap</th>
<th>Dimension</th>
<th>Power Law</th>
<th>Tau-Coupling</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Vision echolocation</td>
<td>$w_0$</td>
<td>distance</td>
<td>$Z$</td>
<td>distance</td>
<td>$w_0 = CZ^{-1}$</td>
<td>$\tau_Z = -\tau_{w_0}$</td>
</tr>
<tr>
<td>2</td>
<td>Vision echolocation</td>
<td>$w$</td>
<td>distance</td>
<td>$Z$</td>
<td>distance</td>
<td>$w = CZ^{-1}$</td>
<td>$\tau_w = -\tau_Z$</td>
</tr>
<tr>
<td>3</td>
<td>Vision echolocation</td>
<td>$w$</td>
<td>distance</td>
<td>$W$</td>
<td>distance</td>
<td>$w = CW$</td>
<td>$\tau_W = \tau_w$</td>
</tr>
<tr>
<td>4</td>
<td>Vision echolocation</td>
<td>$\theta$</td>
<td>angle</td>
<td>$\Theta$</td>
<td>angle</td>
<td>$\theta = \Theta$</td>
<td>$\tau_\theta = \tau_\phi$</td>
</tr>
<tr>
<td>5</td>
<td>Vision echolocation</td>
<td>$\phi$</td>
<td>angle</td>
<td>$\phi$</td>
<td>angle</td>
<td>$\phi = \phi$</td>
<td>$\tau_\phi = \tau_\phi$</td>
</tr>
<tr>
<td>6</td>
<td>Vision</td>
<td>$\beta$</td>
<td>angle</td>
<td>$R$</td>
<td>distance</td>
<td>$\beta = CR^{-1}$</td>
<td>$\tau_\beta = -\tau_\beta$</td>
</tr>
<tr>
<td>7</td>
<td>Echolocation</td>
<td>$d$</td>
<td>time</td>
<td>$R$</td>
<td>distance</td>
<td>$d = CR$</td>
<td>$\tau_d = \tau_d$</td>
</tr>
<tr>
<td>8</td>
<td>Echolocation</td>
<td>$i$</td>
<td>sound intensity</td>
<td>$R$</td>
<td>distance</td>
<td>$i = CR^{-1}$</td>
<td>$\tau_i = -\mu \tau_i$</td>
</tr>
<tr>
<td>9</td>
<td>Electrocution</td>
<td>$u$</td>
<td>voltage</td>
<td>$D$</td>
<td>distance</td>
<td>$u = CD^{-1.7}$</td>
<td>$\tau_D = -1.7 \tau_u$</td>
</tr>
<tr>
<td>10</td>
<td>Electrocution</td>
<td>$p$</td>
<td>voltage</td>
<td>$R$</td>
<td>distance</td>
<td>$p = CR^{-2}$</td>
<td>$\tau_p = -2 \tau_p$</td>
</tr>
<tr>
<td>11</td>
<td>Infrared vision</td>
<td>$h$</td>
<td>infrared intensity</td>
<td>$R$</td>
<td>distance</td>
<td>$h = CR^{-2}$</td>
<td>$\tau_h = -2 \tau_h$</td>
</tr>
</tbody>
</table>
any other frame of reference (and, as shown earlier, one has to be set up) would result in more complex sensory specification (see Bootsma & Oudejans, 1993; Tresilian, 1994). Thus, it is likely to be more efficient to first set up an effective frame of reference to make the sensory specification straightforward.

Rows 4 and 5: Here sensory specification is straightforward, because the sensory angles $\theta$ and $\phi$ are the same as the motion angles $\Theta$ and $\Phi$, respectively.

Row 6: $\beta$ is a small angle subtended at $O$ by any two elements in the vicinity of $P$ that lie in a line perpendicular to the plane $OZP$. ($\beta$ is not shown in Figure 2). In the power law equation, $C$ equals the distance between the two elements. Assuming the animal does not "know" this distance then $\beta$ cannot specify $R$. However, $-\tau_\theta$ does specify $\tau_R$ through the tau-coupling equation.

Row 7: $d$ is the delay, measured at the head of an echolocating animal (e.g., a bat), between its cry and the returning echo. Constant $C$ in the power law equation equals $2/v_c$ where $v_c$ is the velocity of sound in the ambient medium. If the animal "knew" the value of $v_c$ then the sensory gap $d$ would specify the motion gap $R$ through the power law equation. In all events, $\tau_d$ equals $\tau_R$ through the tau-coupling equation (Lee, van der Weel, et al., 1992).

Row 8: $i$ is the sound intensity of the returning echo, measured at the head of an echolocating animal. $C$ in the power law equation depends on the sound-absorbing properties of the medium and reflecting surface and is unlikely to be knowable by the animal—in which case motion distance $R$ is not specified. $\mu$, however, depends only on the surface geometry of the reflecting surface ($\mu$ ranges in value from about 2 for specular reflection from a flat surface to about 4 for diffuse scattering from a spherical surface), and its value could be "knowable" by the animal for familiar reflecting objects (prey insects, foliage, and the like). $\tau_i$ would then specify $\tau_R$ through the tau-coupling equation (Lee, van der Weel, et al., 1992).

Row 9: $v$ is the change in the transepidermal voltage at the electrosensors in the skin of a weakly electric fish due to change in the distance $D$ of a nearby object. Weakly electric fish live in murky waters and use electrolocation to get around. $C$ in the power law equation (Bastian, 1986) varies with the conductivity and size of the object. If these are unknown to the animal then motion distance $D$ is not sensorily specified. $\tau_D$ is, however, specified by $\tau_v$ through the tau-coupling equation.

Row 10: $p$ is the electric potential registered under water by the array of electrosensors on a platypus's bill, which enable it to locate its prey (e.g., shrimps) by the electric field generated by the prey's muscular activity (Manger & Pettigrew, 1995; Scheich, Langner, Tidemann, Coles, & Guppy, 1986). To a good approximation, $p$ will be proportional to the inverse square of the distance $R$ to the prey, giving the power law relation: $p = CR^{-2}$. $C$ will vary with the level of electrical activity of the prey's muscles; if this is not known to the platypus then distance $R$ is not sensorily specified. $\tau_R$ is, however, specified by $\tau_p$ through the tau-coupling equation.

Row 11: $h$ is the infrared intensity picked up by the array of heat-sensitive nerve fibers in the pit organs of a snake (pit viper or boid snake) due to the presence of a heat-radiating body such as a mouse. The snakes can strike accurately using infor-
mation picked up by the pit organs, which act like eyes and map onto the optic tectum (Newman & Hartline, 1982). C in the power-law equation will depend on the heat-radiating properties of the prey; if these are not known to the snake then motion distance R is not sensorily specified by the power law equation. \( \tau_R \) is, however, specified by \( \tau_k \) through the tau-coupling equation.

**TAU IN ACTION**

To illustrate how tau-coupling might be used in guiding movement, I consider the task of moving a point of observation O with respect to a goal position G or a surface. I show how different types of guidance could, in principle, be achieved by mainly using three basic motion-taus. This is illustrated in Figure 3. They are: (a) \( \tau_{MOG} \), the tau of the "motor angle" \( \Theta_{MOG} \) between the instantaneous direction of motion OM and the direction OG to the goal; (b) \( \tau_G \), the tau of the distance gap \( D_G \) to the goal; (c) \( \tau_{ROG} \), the tau of the "reference angle" \( \Theta_{ROG} \) between a reference direction OR to a distant point R (which acts like a compass bearing) and the direction OG to the goal. In what follows it will be assumed that the motion variables \( \Theta_{MOG} \), \( \tau_{MOG} \), \( \Theta_{ROG} \), \( \tau_{ROG} \), and \( \tau_G \) are sensorily specified and discussion will be confined to the motion variables themselves. How the motion variables could be sensorily specified through tau-coupling has been detailed in Table 1.

Our main concern is not with how any particular animal guides its movement but rather with trying to understand the general information and procedures that could

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**FIGURE 3** Showing the two angular gaps (\( \Theta_{MOG} \) and \( \Theta_{ROG} \)) and the distance gap (\( D_G \)), the taws of which (\( \tau_{MOG} \), \( \tau_{ROG} \), and \( \tau_G \)) provide tools for controlling steering.
be used by any animal (or robot) for guiding movement. Though different species may get around in different ways, as may different individuals as a result of learning, it nonetheless seems likely that most, if not all, animals may have similar tools for guidance at their disposal. The guidance procedures used may be algorithmic (guaranteeing a result) and/or heuristic (rule of thumb). Several heuristic procedures for guiding movement have been proposed in the literature (e.g., Land & Collett, 1974; Srinivasan, Zhang, Lehrer, & Collett, 1996; see also Beall & Loomis, 1997). Here, however, we confine attention to delineating possible algorithmic procedures.

**Steering to Goals**

*Steering curved and straight courses.* Movement to a goal may be guided just in terms of \( \tau_{MOG} \). 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 4a). Insects have been observed to follow such a spiral toward a candle (Buddenbroek, reported in Thompson, 1966). Pilots of light aircraft use the strategy to spiral down to an airstrip (the trick is to keep 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.

![Figure 4a](image)

![Figure 4b](image)

**FIGURE 4** (a) Steering to a goal by keeping \( \tau_{MOG} \) infinite (or \( \Theta_{MOG} \) constant) results in an equi-angular spiral course (notation as in Figure 3). (b) A more efficient procedure is to keep \( \dot{\tau}_{MOG} = k = \text{constant} \) (0 < \( k \) < 1), which results in turning onto a straight course to the goal. The path shown was generated by starting with \( \Theta_{MOG} = 60^\circ \) and keeping speed constant and \( \dot{\tau}_{MOG} = 0.4 \).
Consider now the more direct procedure of changing the direction of motion to move as directly as possible to a goal. It basically requires shifting the center 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.) It is essentially a gap-closing problem, and so similar to stopping at traffic lights. Thus, one way of closing the motion angle $\Theta_{MOG}$ (Figure 3), so that its closure rate tends to zero as it tends to zero, would be to start $\Theta_{MOG}$ reducing and then keep $\dot{\Theta}_{MOG} = k$ for some constant $k$ lying between zero and 0.5 (see previous section on $\dot{\tau}$). The consequence of doing this is illustrated in Figure 4b. The course swings around, reducing the motion angle $\Theta_{MOG}$ at a decelerating rate, until the course settles on a straight line toward G with $\Theta_{MOG} = 0$.

**Steering a circular arc.** A linear course may be viewed as a limiting case of a circular course, because both types of course require holding constant the force applied perpendicular to the instantaneous direction of motion. The force is zero for the linear course and positive (centripetal) for the circular course. Moreover, maintaining a linear course, as with a steering wheel, normally involves movements along short circular arcs. Thus, it is instructive to consider how movement along circular paths might be guided.

Figure 5 shows a point of observation O on a circular course. G is an arbitrary point on the course. OR is a reference direction (like a compass bearing) in the plane of motion that lies angularly close to the instantaneous direction of motion OM; that is, angle ROM is small. The distant reference point R may be periodically changed during the motion to satisfy this criterion. The reference angle $\Theta_{ROG}$ between RO and OG and the motion angle $\Theta_{MOG}$ between the instantaneous direction of motion OM and OG are both particularly relevant to steering a circular course. For if G is on the circular course, $\tau_{ROG}$ and $\tau_{MOG}$ are tau-coupled. In particular, $\tau_{MOG} = -\tau_{ROG}$. On the other hand, $\tau_{MOG} \neq -\tau_{ROG}$ for points off the course.  

Thus the potential circular course (if steering angle were not changed) is specified by the set of points for which $\tau_{MOG} = -\tau_{ROG}$. Warren, Mestre, Blackwell, and Morris (1991) showed in a simulator experiment that humans can perceive direction of circular heading with respect to a destination point to an accuracy of 1.5°, even with just a few texture elements on the ground. It is possible the participants used the tau information, but that would need to be tested. The tau information could also, in principle, be used to control braking along the circular arc, because

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2The proof is as follows. Referring to Figure 5, from simple geometry, angle $MOG = 90^\circ$ and angle $OCG = \text{twice angle } MOG (2\Theta_{MOG})$. Thus the rate of rotation of OM relative to the fixed direction CG equals $2\Theta_{MOG}$. But the rate of rotation of OM relative to the other fixed direction OR equals $(\Theta_{MOG} - \Theta_{ROG})$. Hence, $2\Theta_{MOG} = (\Theta_{MOC} - \Theta_{ROG})$; that is, $\Theta_{MOC} = \Theta_{ROG}$. Therefore, when $\Theta_{ROG} = \Theta_{MOC}$, $\tau_{ROG} + \tau_{MOG} = 0$. Following similar reasoning it is easy to show that, for any point lying on the outside of the circular course, $\tau_{MOG} + \tau_{MOG} > 0$ and for any point lying on the inside $\tau_{ROG} + \tau_{MOG} < 0$. It also follows from the aforementioned that the time-to-arrival of O at G at the current approach rate = (angle OCG)/(rate of change of angle OCG) = $(2\Theta_{MOG})/(2\Theta_{MOG}) = \tau_{MOG}$.
the value of $\tau_{MOG}$ for a point $G$ on the arc equals the time-to-arrival of $O$ at $G$ at the current closure rate. In other words, $\tau_{MOG} = \tau$ of the circular arc gap between $O$ and $G$. Braking could therefore be controlled by keeping $\tau_{MOG}$ constant.

Steering and controlling speed. This could, in fact, be achieved by a single tau-coupling, namely $\tau_G = k \tau_{MOG}$, for constant $k$, $0 < k < 1$ (Figure 6). It follows from the tau-coupling theorem (Appendix A) that maintaining the tau-coupling $\tau_G = k \tau_{MOG}$ would ensure that, as $\Theta_{MOG}$ tended to zero, gap $D_G$ would tend to zero and its closure rate would then be close to zero. To be more specific, for $0 < k < 0.5$, 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 6.

Negotiating Obstacles

Rounding obstacles. A course may be steered around an obstacle using just $\tau_{MOG}$. A squirrel running around a tree is one example. Another is steering a vehicle around a bend in a road. The bend may be steered using $\tau_{MOG}$ by taking the (moving)
tangent point on the inside edge of the road or lane as the goal (Figure 7a). If the bend were of constant curvature, as many road bends are, then keeping $\tau_{MOG}$ infinite (or $\Theta_{MOG}$ 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 center of curvature.

**Swinging into bends.** Racing drivers swing into bends, as do most drivers to a certain extent. It requires decreasing $\Theta_{MOG}$ (the angle to the tangent point) to a lower value (Figure 7b). This gap-closing problem could be solved in a similar way as steering onto a straight course, as described earlier. In the present case the goal value of $\Theta_{MOG}$ is likely to be a small value ($\Theta^*_{MOG}$ say) rather than zero, so as to avoid contacting the inside edge of the road. Then the gap would be $(\Theta_{MOG} - \Theta^*_{MOG})$ rather than $\Theta_{MOG}$ and the procedure would be to keep $\dot{\tau}(\Theta_{MOG} - \Theta^*_{MOG})$ constant. I have data, not yet published, that support this hypothesis. Land and Lee (1994) found that drivers tended to fix gaze on the tangent point as they approached and entered a bend. It is possible that this would facilitate the pick-up of $(\Theta_{MOG} - \Theta^*_{MOG})$.

**Controlling Final Approach**

**Asymptoting on surfaces.** The problem we now consider is steering to a flat surface and arriving moving parallel to it. Examples are a bird or airplane pilot landing on the ground or water, or a driver straightening out of a bend. Figure 8 diagrams two versions of the problem: (a) where the contact point is specified and (b) where it is unspecified. In Case a, as $O$ reaches goal $G$ and $D_G$ becomes zero, the angle $\Theta_{OGS}$ also has to reach zero. In principle, this could be achieved by tau-coupling $\tau_{OGS}$ (the $\tau$ of $\Theta_{OGS}$) and $\tau_G$ (the $\tau$ of $D_G$). A problem would seem to be sensing $\tau_{OGS}$. However, this turns out not to be necessary. It would be sufficient to tau-couple $\tau_R$ and $\tau_G$, both of which could, in principle, be sensed (see Table 1). This tau-coupling, when angle $\Theta_{OGS}$ is small, would, in fact, automati-
FIGURE 7 (a) Rounding a cylindrical part of an obstacle keeping $\tau_{MOG}$ infinite (or $\Theta_{MOG}$ constant) results in motion along a concentric path. The arrow lines indicate the instantaneous directions of motion, OM. (b) Swinging into a bend. Keeping $\tau(\Theta_{MOG} - \Theta_{MO})$ constant results in $\Theta_{MOG}$ getting progressively smaller until it stabilizes on its goal value $\Theta_{MOG}$.

cally ensure that $\tau_{OOS}$ and $\tau_G$ were tau-coupled. Asymptoting at an unspecified point (Figure 8b) could be solved in a similar way by tau-coupling $\tau_R$ and $\tau_M$. When angle $\Theta_{OMS}$ is small, this would ensure that $\tau_{OMS}$ and $\tau_M$ were tau-coupled (proof similar to footnote 3), which would make the angle of approach to the surface zero at contact.

**Arriving from the right direction and stopping.** It is often necessary to move to the right 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? We end this section with the elegant feat performed by an echolocating bat (*Eptesicus fuscus*) in flying across a room to land on a finger (Figure 1a). The bat has to stop at the finger and approach it from the right direction so that it can somersault and alight upside-down. Analysis of the bat’s flight path revealed that it approached the finger from a consistent direction (46° ± 4° to the vertical) and that its speed was close to zero as it arrived (Lee et al., 1995). The analysis further indicated that it achieved the feat by simultaneously following two tau procedures. One procedure was keeping constant $\tau_X$ (τ of the gap X to the finger). This ensured that its velocity was virtually zero as it reached the finger. The other procedure was keeping $\tau_A$ (τ of the angle

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3Proof. Applying the single rule to triangle OPG in Figure 8 gives $D_R \cdot \sin \Theta_{OOGS} = D_O \Theta_{OOGS}$. Differentiating the equation with respect to time and elimination $\Theta_{ORS}$ (which is constant) between the two equations yields $1/\tau_{R} = 1/\tau_G + 1/\tau_{OOGS}$. 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 $\tau_G = (k - 1)\tau_{OOGS}$. That is, $\tau_G$ and $\tau_{OOGS}$ are tau-coupled.
A between the current direction to the finger and the goal direction on arrival) coupled onto $\tau_x$. This ensured that as it stopped at the finger angle $A$ became zero.

**INTRINSIC TAU-GUIDANCE**

We have seen how the complete trajectory to a goal can be generated and controlled, not explicitly but implicitly, by coupling extrinsic motion-taus ($\tau_G$, $\tau_{MOG}$, $\tau_{ROG}$, and so on), the values of which could be sensed by the animal. However, there is more to guidance of movement than is afforded by extrinsic variables. This becomes apparent when we consider the problems of timing arrival at a goal and controlling the force and momentum at arrival. These are important problems for a cat pouncing on a scurrying mouse, and are for someone playing a piano. Each has to arrive at the right place at the right time in the right way. The movement is prescribed by the mouse in one case and by the flow of the music in the other.

Playing music is a good case to examine because the task is well defined. The music imposes explicit constraints on the spatial, temporal, and dynamical form of the
movement. Consider, for example, someone playing piano in a group, listening to their fellow players, and waiting for the moment to come in with a chord. They have to strike the keys at just the right time to fit in with the beat of the music, on just the right notes to create the chord, and with just the right momentum and force to achieve the appropriate loudness and resonance of sound. How do they do it?

We have shown how steering to the right places—the notes in this case—might be accomplished by tau-coupling. The problem of bringing the fingers down on the notes at the same time can also be solved by tau-coupling—by coupling the taus of the gaps between the fingers and the notes (see previous section on tau-coupling). But how are the fingers brought down in time with the beat of the music? There is no extrinsic motion-tau onto which the tau of the gap between fingers and notes might be coupled to guide the movement. Rather, the player has effectively to extrapolate the time of the next beat, from hearing the last beat and the recent interbeat interval (which, of course, may not be constant because of changes in tempo), and guide their movement so that it ends at that time. It would seem, therefore, that playing on the beat is not explicable in terms of tau-coupling onto extrinsic motion-tau alone.

The nervous system is, however, clearly implicated in guiding movement moment by moment, as Bernstein (1967) argued, and as has been demonstrated, for example, in experiments on the function of the motor cortex in prescribing direction of movement (Georgopoulos, 1995; Georgopoulos, Kalska, Crutcher, Caminiti, & Massey, 1984) and in analysis of the function of the cerebellum (Stein & Glickstein, 1992). If neural processes have evolved to guide movements using tau-coupling of extrinsic taus, it is feasible that the same processes might be deployed in guiding a movement, even when there is no extrinsic tau to guide it. What would be required is that the nervous system generate its own tau to guide the movement, using (in the case of piano playing) the acoustic information about the musical beat to set the parameters of this intrinsic tau-guide. The tau of the movement would be tau-coupled onto the intrinsic tau-guide in a similar way as tau-coupling onto an extrinsic tau. The only difference would be that information about the extrinsic tau would come through the senses whereas the intrinsic tau-guide would be generated within the nervous system.

**Second-Order Intrinsic Tau-Guides**

Assuming that evolution tends to opt for simple robust processes, we may ask: What would be the simplest type of intrinsic tau-guide that would be adequate for the job? In general terms, an intrinsic tau-guide is conceived as simply a time-varying value generated by a bodily process. It may be thought of as a "graph" of tau against time. When used to guide a movement to a goal, the motion-tau would be constantly tau-coupled onto the tau-guide.

To aid visualization, and without losing generality, the tau-guide's "graph" may be considered to be generated by some quantity, q, such as electrical charge, flowing out of a reservoir of fixed capacity in the body at some controlled (but varying) rate; the
value of the tau-guide at any moment would be the time-to-being-empty of the reservoir at the current emptying rate. A flow function that would require minimum specification, and yet be versatile for generating useful tau-guides, would be one where the second-order time derivative of the quantity was constant (and so higher orders of time derivative were zero). An intrinsic tau-guide generated by such a function is referred to as a second-order intrinsic tau-guide, and is designated $\tau_{e}$.

The set of second-order intrinsic tau-guides includes, as a special subset, those where the second-order time derivative of the quantity is zero (and so flow-rate is constant). These will be referred to as zero-second-order intrinsic tau-guides, and designated $\tau_{e_{0}}$.

Second-order intrinsic tau-guides, therefore, have a single adjustable parameter, corresponding to the value of $\dot{q}_{d}$, the (constant) second-order time derivative of the quantity $q_{d}$. Zero-second-order intrinsic tau-guides also have a single adjustable parameter, corresponding to the flow-rate, $\dot{q}$, of the quantity $q_{d}$. Alternatively, the adjustable parameter may be considered, in each case, to be $\delta$, the duration of the tau-guide. This is because $\dot{q}_{d}$ and $\delta$ (and $\ddot{q}_{d}$ and $\delta$) are mutually equivalent because $\dot{q}_{d} = 2C/\delta^{2}$ (and $\ddot{q}_{d} = C/\delta$), where $C$ is the (fixed) capacity of the reservoir.

In summary, the second-order intrinsic tau-guide hypothesis is concerned with explaining intrinsic aspects of movement guidance, as compared with the online extrinsic guidance by perceptual variables discussed earlier in this article. The hypothesis is that in the intrinsic guidance of movement, $\tau_{M}$, the tau of a motion gap (e.g., between fingers and piano keys) is tau-coupled, at each time $t$, onto a second-order intrinsic tau-guide, $\tau_{e}$, such that

$$\tau_{M} = k\tau_{e}$$

(3)

where $k$ is a constant. In Appendix B, the equation for $\tau_{e}$ is derived, together with the equations for the motion-tau, the motion gap, the gap closure rate and the rate of change of closure rate that would result from the tau-coupling in Equation 3. The curves representing those equations are plotted, for different values of $k$, in Figure 9.

It is noted that, when using a second-order intrinsic tau-guide to guide movement across a distance gap, the tau-guide generates a motion that first accelerates and then decelerates (Figure 9d). Thus the kinematics that emerge from tau-coupling

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4 To see why a second-order intrinsic tau-guide generates an acceleration followed by a deceleration, consider Figure 9a. That shows, for different values of $k$, the plots of movement-tau against time. From Equation 3, movement-tau equals $k\tau_{e}$. The lowest thickest curve in Figure 9a is the plot of $k\tau_{e}$ when $k = 1$ (i.e., the plot of $\tau_{e}$). Successively higher and thinner curves are plots of $k\tau_{e}$ for progressively smaller values of $k$. Each curve starts off steeply and gets progressively less steep. That is, the gradient of each curve ($k\tau_{e}$ = $\tau_{M}$) starts off greater than 1 and progressively reduces through the value of 1 (a gradient of 1 is represented by the diagonal line). Now a value of $\tau_{M} > 1$ means that the movement is accelerating, and a value of $\tau_{M} < 1$ means it is decelerating (Lee, 1976). Thus as the gradient of a movement-tau curve passes through a value of 1 (when the tangent to the curve is parallel with the diagonal line in Figure 9a, as indicated by the arrows) the movement shifts from accelerating to decelerating. The times when this occurs corresponds to the times of the peak velocities (Figure 9c) and of the acceleration zero-crossings (Figure 9d).
FIGURE 9  (a) Motion-tau, (b) motion gap, (c) gap closure rate, and (d) rate of change of gap closure-rate profiles of a motion from rest that would result if the motion-tau, $\tau_{m}$, were tau-coupled, at each time $t$, onto a second-order intrinsic tau-guide, $\tau_{g}$, by keeping $\tau_{m} = k \tau_{g}$ for a constant $k$ (details in Appendix B). The profiles, normalized so that the extent and duration of motion is unity, are shown for five different values of $k$. In general, peak closure rate is reached later in the motion and the rate of change of closure rate is greater, the higher the value of $k$ (for $0 < k < 1$). The arrows on the graph lines indicate where the slope of the graph is unity (and the tangent to the graph is parallel to the $45^\circ$ line shown). This is when the peak closure rates occur.

onto the guide (Equation 3) are sigmoid gap profiles (Figure 9b) and bell-shaped velocity profiles (Figure 9c), which are typical of, for example, skilled reaching movements. The value of $k$ in the tau-coupling (Equation 3) determines relevant kinematics of the movement. In particular, for $k$ lying between 0 and 1, the larger the value of $k$, the longer the duration of the acceleration phase of the movement and the more abrupt the deceleration to the goal (Figure 9d).
Evidence suggesting the existence of zero-second-order intrinsic tau-guides has, in fact, been around for some time, though in disguise. As pointed out earlier in the section on stabilizing $\dot{t}_Y$ and discussed in more detail in Appendix B, using a zero-second-order intrinsic tau-guide to guide a movement is equivalent to keeping $\dot{t}_Y$ constant—and there is quite a lot of evidence suggesting that $\dot{t}_Y$ is kept constant when decelerating toward a goal (e.g., Lee et al., 1993; Lee et al., 1991; Lee et al., 1995; Lee, van der Weel, et al., 1992; Lee, Young, et al., 1992; Yilmaz & Warren, 1995).

Recently, the general second-order intrinsic tau-guide hypothesis has been tested against movement data by calculating the proportion of variance in a motion-tau, $\tau_m$, that is accounted for by the predicted relation $\tau_m = k \tau_p$. So far we have tested the hypothesis on four different activities and have obtained supportive evidence on each (mean proportion of variance accounted for was greater than 0.98). These include control of suction by newborns bottlefeeding (Craig & Lee, 1998), control of movement of the hand to mouth by adults when eating with eyes closed (Lee, Craig, & Grealy, 1998), control of movement of the foot from one footfall to the next when sprinting (Lee, Grealy, & Rewt, unpublished data), and control of movement of the hand to drum of a Nigerian master drummer (Noble, 1998). Thus the hypothesis appears to be valid for self-paced as well as musically constrained movements. This makes sense, because musical movements are, presumably, a refined expression of more basic underlying abilities.

**CONCLUDING REMARKS**

When negotiating the cluttered environment, animals normally control their movement with graceful speed and agility. Indeed, inability to do so would often, in the long run, be fatal. A large nervous system is not necessary. Insects and other small animals show fine ability in guiding their movements. It is likely, therefore, that movement guidance is based on relatively simple principles and carried out by smart perceptuomotor processes that have evolved for the tasks in hand.

Building on J. J. Gibson's ideas, as expressed particularly in his classic 1958 article, I have outlined a theory of sensory guidance of movement. The theory is based on four main principles:

1. A central task in guiding movement is controlling the closure of spatial and/or force gaps between effectors (or sensory organs) and their goals.
2. This requires sensing the closure of gaps in sensory input arrays, for example, optical (vision), acoustic (echolocating bats), force (haptics), electrical (electrolocating fish and platypi), and electromagnetic (infrared detection by snakes).
3. The tau of each spatial and/or force gap—the time-to-closure of the gap at its current closure rate—is basically what is sensed and controlled constantly to guide the movement.

4. A principal method of movement guidance is by tau-coupling the taus of different gaps, that is, keeping the taus in constant ratio.

I have shown theoretically how tau-coupling could be used to synchronize the closure of gaps and to regulate the kinematics of closure. Experiments supporting the idea have been reported. In addition, it has been shown that the braking procedure of keeping \( \tau_x \) constant, for which there is also empirical support, can be viewed as a particular case of tau-coupling.

As regards to how taus of motion gaps might be sensorily specified, I demonstrated that they could, through tau-coupling, be specified by sensory-taus, defined on sensory arrays. How this principle could apply to a range of different perceptual systems has been detailed. There is supportive evidence from visual experiments. Experiments in other sensory modalities need to be done.

Applying the theory to the problem of guiding steering, I showed how tools for steering could be built from tau-couplings and how these would enable steering control in a variety of situations. The steering tasks considered include steering straight or curved courses to destinations, controlling steering and speed together, negotiating obstacles, and steering asymptotic paths to surfaces as when landing or exiting from a bend in the road. There is supportive evidence for some of these ideas, but further experiments are required.

Guidance of movement cannot, however, be explained fully in terms of extrinsic variables. Intrinsic guidance of movement also plays an important role. This is perhaps most evident in musical performance, where the player's movements have to fit the rhythms and dynamics of the music, the information about which is partly or wholly internalized. A hypothesis has been developed to help explain intrinsic guidance of movement within the same theoretical framework as extrinsic guidance. I showed theoretically how both the timing and the acceleration and deceleration phases of a movement could be controlled by tau-coupling the tau of the movement onto a (hypothesized) second-order intrinsic tau-guide. There is empirical evidence from a small range of activities, both musical and nonmusical, supporting the hypothesis, but again more experiments are needed.

The ideas also need to be tested and developed at the neurophysiological level. Cerebellum, basal ganglia, superior colliculus, parietal cortex, motor cortex, and muscle spindles are some of the areas that it would probably be worthwhile investigating in this way.

It seems possible that tau-couplings might also help to tie the different movement components of an action together to form a smoothly coordinated whole. Which particular tau-couplings are formed would depend on how a skill is developed. Thus, the theory could be useful in studying normal development, in diag-
nosing and treating abnormal development, in skill training, and in rehabilitation (Lee, von Hofsten, & Cotton, 1997; van der Weel, van der Meer, & Lee, 1996).

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**APPENDIX A**

**Tau-Coupling Theorem**

1. If gaps $x$ and $y$ are tau-coupled—i.e., $\tau = k\tau_y$ for a constant $k$—then $y = Cx^{1/k}$ (assuming, without loss of generality, that $x > 0$).
2. Considering now what happens when gap $x$ closes, i.e., $x \to +0$:
   a. If $k<0$, as $x \to +0$, gap $y$ theoretically opens to infinity, because $y \to +\infty$, $\dot{y} \to +\infty$, $\ddot{y} \to \pm \infty$. In practice, $\dot{y}$ and $y$ will stay finite because $\ddot{y}$ will reach a maximum level.
b. If \(0 < k < 0.5\), as \(x \to +0\), gap \(y\) closes, closure rate of \(y\) becomes zero, and rate of change of closure rate becomes zero, because \(y \to +0, \dot{y} \to -0, \ddot{y} \to \pm 0\).

c. If \(0.5 < k < 1\), as \(x \to +0\), gap \(y\) closes, closure rate of \(y\) theoretically becomes zero and rate of decrease of closure rate theoretically becomes infinite, because \(y \to +0, \dot{y} \to -\infty, \ddot{y} \to \pm \infty\). In practice, closure rate will stay finite because the rate of decrease of closure rate will reach a maximum level.

d. If \(1 < k\), as \(x \to +0\), gap \(y\) closes, closure rate becomes infinite and rate of change of closure rate becomes infinite, because \(y \to +0, \dot{y} \to -\infty, \ddot{y} \to \pm \infty\). In practice, the rate of change of closure rate will reach a maximum level, and so closure rate will stay finite.

**Proof 1.** If \(\tau_y = k\tau_x\), then by definition of tau

\[
y / \dot{y} = k (x / \dot{x}) \tag{A1}
\]

By inverting \(y\) and \(\dot{y}\), the equation becomes

\[
\dot{y} / y = (1/k) (\dot{x} / x) \tag{A2}
\]

and integrating with respect to time

\[
\log y = (1/k) \log x + \log C \tag{A3}
\]

where \(C\) is a constant. Thus

\[
y = Cx^{1/k} \tag{A4}
\]

**Proof 2.** Differentiating Equation A4 with respect to time

\[
\dot{y} = C (1/k) x^{(1/k) - 1} \dot{x} \tag{A5}
\]

Differentiating again with respect to time

\[
\ddot{y} = C (1/k) x^{(1/k) - 2} \left[ \left( (1/k) - 1 \right) \dot{x}^2 + x \ddot{x} \right] \tag{A6}
\]

Now consider what happens to \(y\), \(\dot{y}\), and \(\ddot{y}\), as \(x \to +0\).
1. If \( k < 0 \), then \( 1/k < 0 \) and so the exponent of \( x \) will be negative in Equations A4, A5 and A6. Thus, as \( x \to +0 \), \( y \to +\infty \), \( y \to +\infty \), and \( \dot{y} \to \pm \infty \).

2. If \( 0 < k < 0.5 \), then \( 1/k > 2 \) and so the exponent of \( x \) will be positive in Equations A4, A5 and A6. Thus, as \( x \to +0 \), \( y \to +0 \), \( \dot{y} \to -0 \), and \( \ddot{y} \to \pm 0 \).

3. If \( 0.5 < k < 1 \) then \( 1 < 1/k < 2 \) and so the exponent of \( x \) will be positive in Equations A4, A5 and negative in Equation A6. Thus, as \( x \to +0 \), \( y \to +0 \), \( \dot{y} \to -0 \), and \( \ddot{y} \to \pm \infty \).

4. If \( 1 < k \) then \( 0 < 1/k < 1 \) and so the exponent of \( x \) will be positive in Equation A4, and negative in Equations A5 and A6. Thus, as \( x \to +0 \), \( y \to +0 \), \( \dot{y} \to -\infty \), and \( \ddot{y} \to \pm \infty \).

**APPENDIX B**

**Second-Order Intrinsic Tau-Guides**

The hypothesis is concerned with explaining intrinsic aspects of movement guidance, as compared with online extrinsic guidance by perceptual variables. The hypothesis is that, in the intrinsic guidance of movement, \( \tau_M \), the tau of a motion gap (a spatial or force gap) is tau-coupled, at each time tau, onto a "second-order intrinsic tau-guide," \( \tau_\tau \), such that

\[
\tau_M = k \tau_\tau \tag{B1}
\]

where \( k \) is a constant. Both \( \tau_M \) and \( \tau_\tau \) change over time.

A general intrinsic tau-guide is conceived as simply a time-varying value—a graph of tau against time—generated by a bodily process. Without loss of generality, the graph of a second-order intrinsic tau-guide may be considered to be generated by some quantity, \( \dot{q}_\tau \), such as electrical charge, flowing out of a (full) reservoir of fixed capacity in the body in such a way that the second-order time derivative, \( \ddot{q}_\tau \), of the quantity (i.e., rate of change of flow rate) is constant. The value of the tau-guide at any moment would then be the time-to-being-empty of the reservoir at the current emptying rate. If the reservoir starts emptying at time \( t = 0 \) with zero (first-order) flow rate and with constant second-order flow rate, \( \ddot{q}_\tau \), and is empty after duration \( \delta \), then the initial amount in the reservoir will have been \( \frac{1}{2} \ddot{q}_\tau \delta^2 \). After time \( \tau \) the amount in the reservoir will have been reduced by \( \frac{1}{2} \ddot{q}_\tau \tau^2 \) and so will be equal to

\[
q_\tau = \frac{1}{2} \ddot{q}_\tau \left( \delta^2 - \tau^2 \right) \tag{B2}
\]

The rate of emptying at time \( t \) will be equal to \( -\dot{q}_\tau \). Therefore, \( \tau_\tau \), the value of the tau-guide at time \( t \), is \( \frac{1}{2} \ddot{q}_\tau (\tau^2 - \delta^2) / \dot{q}_\tau \). (\( \tau \) is conventionally taken as being negative during closure on a goal—in this case the goal is an empty reservoir.) Thus, simplifying
\[ \tau_g = \frac{1}{t} \left( t - \delta^2 / t \right) \]  \hspace{1cm} (B3)

for \( t_0 < t \leq \delta \), where \( t_0 \) is a small positive time (\( t = 0 \) is excluded because \( \tau_g \) is infinite then). Note from Equation B3 that \( \tau_g \) has a single adjustable parameter, its duration \( \delta \).

Thus, if \( \tau_M \), the tau of a motion gap (a spatial or force gap) is tau-coupled, at each time \( t \), onto \( \tau_g \) as per Equation B1 (viz, \( \tau_M = k \tau_g \)) it follows from Equation B3 that during all or most of the time interval \( (t_0, \delta) \)

\[ \tau_M = k \tau_g = \frac{1}{t} \frac{1}{2} k \left( t - \delta^2 / t \right) \]  \hspace{1cm} (B4)

for a constant \( k \).

The equations giving the motion gap, \( x_M \), the gap closure rate, \( \dot{x}_M \), and the rate of change of the closure rate, \( \ddot{x}_M \), as a function of time are obtained by first applying the tau-coupling theorem (Equation A4) to Equation B1, which yields

\[ x_M = C x_g^{(1/k)} \]  \hspace{1cm} (B5)

where \( C \) is a constant. Substituting \( x_g = \frac{1}{2} \tilde{q}_g (\delta^2 - t^2) \) from Equation B2

\[ x_M = C \left[ \frac{1}{2} \tilde{q}_g \left( \delta^2 - t^2 \right) \right]^{(1/k)} = D (\delta^2 - t^2)^{1/k} \]  \hspace{1cm} (B6)

where \( D \) is a constant. Differentiating Equation B6 successively with respect to time

\[ \dot{x}_M = -2D (1/k) t (\delta^2 - t^2)^{(1/k - 1)} \]  \hspace{1cm} (B7)

\[ \ddot{x}_M = 2D (1/k) [(2/k - 1) t^2 - \delta^2] (\delta^2 - t^2)^{(1/k - 2)} \]  \hspace{1cm} (B8)

Finally, we normalize Equations B4, B6, B7 and B8, without loss of generality, by setting the duration, \( \delta \), of the tau-guide equal to 1 and the initial size of the motion gap equal to -1. Since \( D = (\text{initial size of motion gap}) / \delta^{2/k} \) (shown by setting \( t = 0 \) in Equation B6), in the normalized equations \( D = 1/1 = 1 \). Thus, substituting \( \delta = 1 \) and \( D = 1 \) in Equations B4, B6, B7 and B8, the normalized forms of these equations are:

\[ \tau'_M = \frac{1}{2} k (t - 1 / t) \]  \hspace{1cm} (B9)

\[ x'_M = \left( 1 - t^2 \right)^{(1/k)} \]  \hspace{1cm} (B10)
\[ \dot{x}_M' = -2(1/k) t (1 - t^2)^{(1/k-1)} \]  
(B11)

\[ \ddot{x}_M' = 2(1/k) \left[ (2/k - 1) t^2 - 1 \right] (1 - t^2)^{(1/k-2)} \]  
(B12)

where primes designate the normalized values. The motion-tau, motion gap, gap closure rate and rate of change of gap closure rate profiles shown in Figure 9 were generated using Equations B9–B12 respectively.

**Zero-second-order intrinsic tau-guide.** In this special case of a second-order intrinsic tau-guide the reservoir empties at a constant rate, \(-\dot{q}_s\). Therefore

\[ \tau_s = (t - \delta) \]  
(B13)

\[ q_s = -\dot{q}_s(t - \delta) \]  
(B14)

Again the guide has a single adjustable parameter, its duration \(\delta\). If a motion-tau, \(\tau_M\), were tau-coupled onto this tau-guide so that \(\tau_M = k\tau_s\) then, from the tau-coupling theorem (Appendix A) and Equation B14, \(x_M = C x_t^{(1/k)} = C(\dot{q}_s \delta)^{(1/k)} (1 - t/\delta)^{(1/k)}\). When \(t = 0\), \(x_M = x_M(0) = C(\dot{q}_s \delta)^{(1/k)}\). Therefore, from the preceding two equations we have

\[ x_M = x_M(0) (1 - t/\delta)^{(1/k)} \]  
(B15)

Differentiating successively with respect to time

\[ \dot{x}_M = \dot{x}_M(0) (1 - t/\delta)^{(1/k) - 1} \]  
(B16)

\[ \ddot{x}_M = [x_M(0)^2/\dot{x}_M(0)] (1 - k) (1 - t/\delta)^{(1/k) - 2} \]  
(B17)

(These equations of motion [B15–B17] are the same as equations 4–6 in Lee, Young, & Rewt, 1992, which result from keeping \(\tau_s \equiv k \equiv \text{constant}\)).