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## A perception – action strategy for hummingbirds

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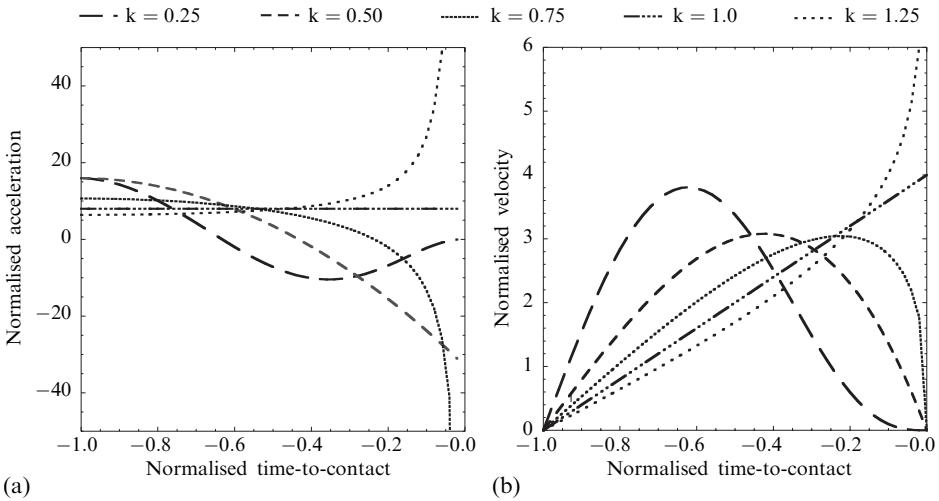
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**Abstract.** Many human and animal tasks are thought to be controlled with the  $\tau$  informational variable. It is widely accepted that controlling the rate of change of  $\tau$  (tau) during decelerative tasks, such as when braking or landing, is one common perceptual control strategy. However, many tasks require accelerating before decelerating to a goal, such as reaching. An advancement of  $\tau$  theory shows how a single action formula may be used to control the full action unit from initiation to peak velocity, and to rest at the goal, with the same perceptual  $\tau$  information as before and accounting for the same decelerative kinematics as before. Here, we test the theory against data from high-speed video of a hummingbird flying to its flower feeder. We find that the theory accounts for 97% of the variance in the data, and thus supports it.

The informational variables that we perceive and use to enact our engagements with the world in movement are not well understood and are a matter of some scientific controversy. One of these variables is the so-called  $\tau$  informational variable, which is said to be a perceptual invariant defined by the rate of closure of a gap to a goal (Lee 1976). Many studies have shown how  $\tau$  information can be perceived and controlled in order to execute successful movements for goal acquisitions. Birds, bees, and even human drivers have all been shown to do it (see Lee 2009). Almost all of the experiments on insect, animal, and human perception by  $\tau$  are based on single decelerations to goals, such as braking to stop a car or landing successfully on one's perch. These are braking paradigms, but  $\tau$  doesn't stop there.

Many natural actions require an initiation to start the movement, giving rise to a peak velocity before the decelerative phase to a goal. An advance on the early  $\tau$  model has been designed to account for this full complement of components in an 'action unit', the new-and-improved  $\tau_G$  model (Lee et al 1999). The model is simple and elegant. It proposes an internal guide ( $G$ ) generated by the nervous system used to 'guide' the perceived  $\tau$  of the ongoing action. The guide works by directly coupling its internal values of  $\tau$  to the externally perceived values of  $\tau$ . Doing so guides the animal from the start, to a peak velocity to the goal, and to rest at the goal, all in one swift action.

Interestingly, the decelerative kinematics produced by the  $\tau_G$  model closely mirrors those produced by the  $\tau$  braking model, the  $\dot{\tau}$  model. This means that the new model retains the same parsimonious sensorimotor efficiency that has been shown at length in the previous literature, but with the important addition of accounting for the initiation phase as well (figure 1). We chose to test this theoretical feature by analysing data that had previously been analysed with the  $\tau$  braking model and where some of the movements also had an initiation phase that was previously unaccounted for. The data we used were of a hummingbird coming to dock at its flower feeder. There were 22 dockings in total, of which 9 were total decelerations without any pauses before the decelerative phase. However, in the other 13, the hummingbird flew to an orienting position roughly horizontal from the flower feeder, slowed to pause, and then made an action toward the flower feeder. We reasoned that the hummingbird may have been



**Figure 1.** Kinematic profiles which result from coupling  $\tau_x$  to the intrinsic  $\tau$ -guide,  $\tau_G$ , at the values shown. If the coupling constant is less than 1.0 but greater than 0, the action begins with maximal acceleration before a reduction of forward momentum to the target. At coupling constants less than 0.5, the animal reduces forward momentum early to decelerate (a), so that the goal is just reached, contacting it with minimal momentum (b). If the coupling constant is greater than 0.5 and less than 1.0, forward momentum is reduced later and deceleration monotonically increases until collision into the goal. If the coupling constant is greater than or equal to 1.0, no deceleration phase occurs. If the coupling constant is greater than 1.0, acceleration monotonically increases until collision into the goal.

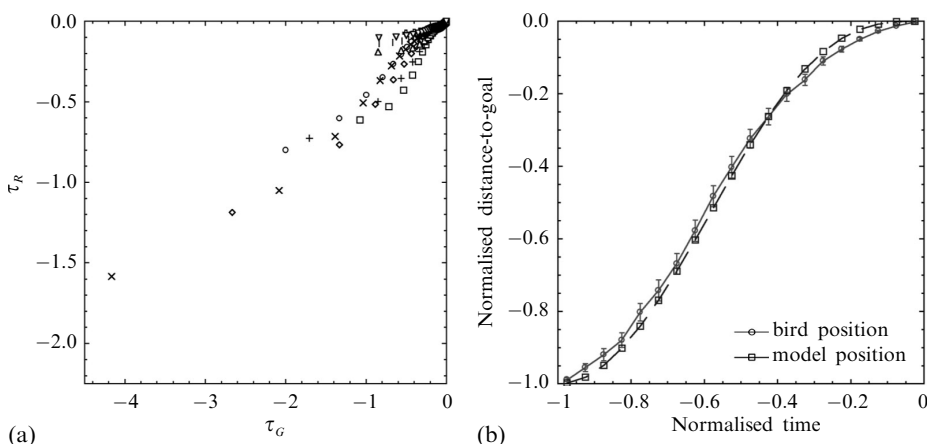
using two strategies: one to control only a decelerative phase to a goal (the  $\tau$  braking model) and another to control the full acceleration-cum-deceleration of the action unit (the  $\tau_G$  model).

To do this, we analysed high-speed (300 feet  $s^{-1}$ ) films of a Sparkling Violet-Ear (*Colibri coruscans*) docking with a horizontal 4 mm diameter feeder tube. The plane of final approach of the bird to the feeder was vertical and closely perpendicular to the optical axis of the movie camera. In total, 22 flights to the feeder were recorded. In 9 of these flights, the hummingbird flew directly to the feeder without stopping. In 13 of these flights, the hummingbird flew to a point parallel in height and about one body-length away from the feeder tube, made an orienting pause with its gaze fixed on the target, and then made the final movement to the feeder. This brought the bird from a hovering position in front of the feeder to a hovering position at the feeder for feeding. We reasoned that this latter set of 13 flights employed a different perceptual guidance strategy to the set where the bird displaced continuously to the feeder without the orienting pause. We analysed these movements. Since the beak-tip, the effector of the hummingbird, is a fixed distance from the eyes, the bird could, in theory, control the docking of the beak into the feeder solely by controlling the optic flow pattern of the beak relative to the feeder at its eyes (Lee et al 1991). Accordingly, we tested whether the discreet acceleration-cum-deceleration movements of the eye were controlled by  $\tau_G$  coupling.

Using a digital tablet (TDS Digitizer, UK), we digitised the films of the 13 movements units to obtain the  $(x, y)$  coordinates of the bird's eye on each frame. For each of the 13 movements, these  $(x, y)$  coordinates were smoothed with a Gaussian filter with a sigma value of 4, and numerically differentiated to obtain the velocity components  $(\dot{x}, \dot{y})$ . The tangential speed,  $S$ , was then calculated on each frame as  $S = \sqrt{(\dot{x}^2 + \dot{y}^2)}$ . The goal position of the eye  $(x_{\text{goal}}, y_{\text{goal}})$ , was taken as the position of the eye on the frame just before  $S$  dropped below 5% of its peak value

during the movement. Similarly, the start of the movement was defined to occur at the frame just after  $S$  rose above 5% of its peak value during the final acceleration, or in the case  $S$  initiated above 5%, its lowest value. For each frame of each movement, the gap,  $R$ , between the eye and its goal position was calculated as  $R = \sqrt{[(x - x_{\text{goal}})^2 + (y - y_{\text{goal}})^2]}$ ;  $R$  was numerically differentiated to give  $\dot{R}$ , and  $\tau_R$  calculated as  $R/\dot{R}$ . For each movement, the duration,  $T$ , was calculated as the time interval between the start and goal frames, and entered into the equation  $\tau_G = 0.5(t - T^2/t)$  to calculate the  $\tau_G$  time series for the movement. The  $\tau_R$  time series was then recursively linearly regressed on the  $\tau_G$  time series, ie if the  $r^2$  of the regression was less than 0.95, the first data point (corresponding to the start of the movement) was removed and the regression re-computed, the process being repeated until  $r^2$  was  $\geq 0.95$ . The percentage of data points remaining measured the ‘percentage of movement  $\tau_G$  coupled’.

We found for the 13 movements that the mean percentage of movement  $\tau_G$ -guided was 96.4%, SD 3.2% (figure 2). The slopes of the regressions provided estimates of the coupling constant,  $k_{X,G}$ , in the  $\tau_G$ -guided movements ( $\tau_X = k_{X,G} \tau_G$ ). The mean value of the slopes was 0.45, SD 0.04. Thus, these data from the 13 docking movements to the flower feeder support the theory that the bird, in this set of cases, was using a visuomotor control strategy that coupled its extrinsic perceptual information on time-to-gap-closure with an intrinsic virtual motor guide. By coupling the changing values of one parameter to the other, the bird appeared to control its acceleration and deceleration to the flower feeder using one simple perception–action mechanism.



**Figure 2.** Experimental data. (a) The bird kept the extrinsic  $\tau_R$  coupled to the intrinsic  $\tau_G$  with a mean coupling constant of 0.45. Marker shapes represent an approach to dock. (b) Normalised distance-to-goal plot of the bird's displacements to the flower feeder (circles), prepared as means (and standard errors) in 20 equidistant time bins. The bird's distance data align with the  $\tau_G$  model with a coupling constant of 0.30 (squares). The small difference with the  $\tau_R/\tau_G$  coupling value, in (a), is due to the mathematics of estimation, because  $r^2 \neq 1$ .

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