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RESEARCH ARTICLE

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Guiding contact by coupling the taus of gaps

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Abstract Animals control contact with surfaces when locomoting, catching prey, etc. This requires sensorily guiding the rate of closure of gaps between effectors such as the hands, feet or jaws and destinations such as a ball, the ground and a prey. Control is generally rapid, reliable and robust, even with small nervous systems: the sensorimotor processes are therefore probably rather simple. We tested a hypothesis, based on general τ theory, that closing two gaps simultaneously, as required in many actions, might be achieved simply by keeping the taus of the gaps coupled in constant ratio. τ of a changing gap is defined as the time-to-closure of the gap at the current closure-rate. General τ theory shows that τ of a gap could, in principle, be directly sensed without needing to sense either the gap size or its rate of closure. In our experiment, subjects moved an effector (computer cursor) to a destination zone indicated on the computer monitor, to stop in the zone just as a moving target cursor reached it. The results indicated the subjects achieved the task by keeping τ of the gap between effector and target coupled to τ of the gap between the effector and the destination zone. Evidence of τ-coupling has also been found, for example, in bats guiding landing using echolocation. Thus, it appears that a sensorimotor process used by different species for coordinating the closure of two or more gaps between effectors and destinations entails constantly sensing the τs of the gaps and moving so as to keep the τs coupled in constant ratio.

Keywords Guidance · Interception · Movement · Tau · Vision

Introduction

It is essential for survival that animals are able to guide the movements of their effectors (hands, jaws, feet, etc.) to objects and places on surfaces, as when grasping things or securing footing when running over rough ground. The guidance has to be prospective. It requires sensory information that is predictive, that allows the ongoing movement to be extrapolated to some degree into the future, so that timely adjustments to the movement can be made to meet the task demands. If the effector is off-course, its motion needs to be adjusted back on course ahead in time.

Guiding contact can require getting to a definite place at the right time. When running over stepping stones, the feet have to be placed accurately at definite places and at the right times in the step cycle. Likewise, playing the piano requires striking the right keys at the right times. Leaping to catch the ball in a rugby line-out, heading a football, and serving at tennis all usually involve timing

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the arrival of the effector (hands, head, racket) at the zenith of its motion to coincide with the ball arriving there.

The force with which an effector makes contact with an object or surface also has to be prospectively controlled. The body has to be moved so that it is in an appropriate posture when the effector makes contact with the surface or object. Thus, coming to an abrupt stop when running requires that the foot contact the ground further ahead of the hips than usual in order to obtain adequate braking force. Similarly, swerving to the left requires the foot to be more to the right at contact in order to be able to generate an adequate leftward force. Hitting a moving or stationary object, as when kicking a football or driving off at golf, likewise requires the body to be in an appropriate posture when contact is made, otherwise the impact could disturb the player's balance or cause injury to the joints, and in all events spoil the action.

In general, then, guiding an effector so that it makes contact with a surface or object at the right place, at the right time and with the right force or velocity of impact requires simultaneously regulating the rates of closure of several gaps: the spatial gap between the effector and surface or object, the spatial gap between the effector and the destination in the environment where interception is to take place, and the gap between the current body posture and the posture to be reached as contact is made. These gaps all have to be reduced to zero, often simultaneously. Controlling how the gaps close usually involves coordinated movement of most of the body.

Experiments on controlling contact with objects and surfaces have addressed movement kinematics and dynamics (Alexander 1997; Bizzi et al. 1992; Flash and Hogan 1985; Jeannerod 1978; Kelso 1995; Schmidt and Turvey 1994), the timing of movement initiation (Bootsma and van Weiringen 1990; Laurent et al. 1994; Port et al. 1997; van der Meer et al. 1994) and the sensory guidance of ongoing movement (Dienes and McLeod 1993; Georgopoulos et al. 1981; Lee et al. 1995, 1997, 1999; McBeath et al. 1995; Milner and Ijaz 1990; Oudejans et al. 1999; Peper et al. 1994; Soechting and Lacquaniti 1983; Zaal et al. 1998). However, no studies have addressed the ubiquitous sensorimotor control problem, outlined above, of guiding an effector so that it contacts an object or surface at the right place, at the right time and with the right velocity or force. That is the subject of the present paper.

Interception task

We investigated sensory guidance of contact in an exacting task where the effector had to be moved to contact a moving object just as it passed through a particular location. In addition, the effector had to be brought to a stop at the moment of contact. The experimental task, which is similar to trapping a moving ball under the foot or hand at a particular location, was run on a computer monitor (Fig. 1). This enabled precise control of the object's motion. The human subject had to move a hand cursor H (the effector) to stop in a circular goal zone centred on a point G on the computer screen just as a moving cursor T (the object to be contacted) reached the goal zone. T moved along a diagonal path at various constant accelerations, decelerations and speeds and H was moved vertically up the screen.

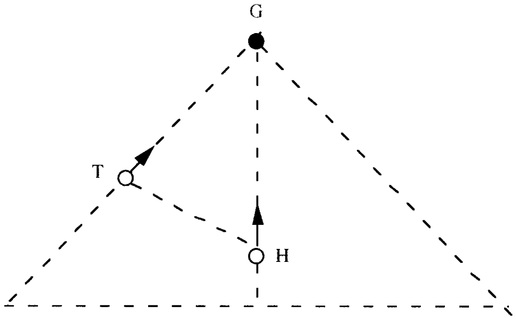

Fig. 1 The experimental task. This required the subject to move a hand cursor H on a computer screen to stop in goal zone G just as the moving target cursor T reached G

τ-coupling

We aimed to test the hypothesis that guidance of contact of the form considered in the experiment is achieved by 'τ-coupling'. (Previous analyses of performance on the experimental task considered other aspects of movement control: Lee et al. 1997; Port et al. 1997.) τ-coupling is an aspect of general τ (tau) theory (Lee 1998). The theory was developed from the theory of τ proposed by Lee (1976), which is a special case of the general theory. General τ theory proposes the following: (1) a central task in guiding movement is controlling the closure of physical gaps between effectors (or sensory organs) and their goals – e.g., distance gaps as when reaching, angular gaps as when redirecting gaze, and force gaps as when gripping something. (2) Online guidance of closure of a gap can be achieved by continuously sensing a single variable, namely the time-to-closure of the gap at the current closure-rate. This is referred to as τ of the gap. It is not necessary to sense the changing size of the gap or its rate of closure, for example. (3) The τs of physical gaps can, in principle, be directly sensed through the τs of corresponding sensory gaps between elements in optic, acoustic and other sensory input arrays. [In the original version of the theory (Lee 1976), the term τ referred only to gaps in the optic flow field corresponding to the gap between the eye and a surface.] (4) A principal means of guiding movement, including closing two physical gaps synchronously, could be by τ-coupling the τs of gaps, i.e., keeping the τs in constant ratio.[1] Evidence supporting the idea of τ-cou-

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[1] More complex couplings, such as systematically varying over time the ratio between two τs or maintaining a power law relation between them, are not considered in the current form of the theory on the grounds that more complex hypotheses should be introduced only when found to be necessary.

pling, ranging from control of flight in echolocating bats to control of nutritive sucking in human neonates, is reviewed in Lee (1998) and discussed later in the present paper.

To illustrate the idea of τ-coupling, consider the two gaps, HG and TG, in the experimental task (Fig. 1). To achieve the task, these gaps have to close simultaneously. Even though the gaps will generally differ in size during the course of the movement and will be closing at different speeds, they could be closed simultaneously simply by keeping the τs of the gaps, τ_{HG} and τ_{TG}, τ-coupled in constant ratio, such that:

$$\tau_{HG}=k\tau_{TG} \qquad (1)$$

1 for a constant *k*. This is because, as gap TG closes, τ_{TG} becomes zero, and so if Eq. 1 holds, τ_{HG} and HG become zero at the same time. Additionally, it can been shown (Lee 1998) that the parameter *k* regulates aspects of the terminal kinematics of closure of the HG gap.

Hypotheses

There are two τ-coupling procedures that might be employed to solve the task:

Procedure 1

Keep $\tau_{HG}=k\tau_{TG}$ (where $\tau_{HG}=\tau$ of gap HG, etc., and *k* is a constant). For $0<k<1$ this would result in H arriving in goal zone G simultaneously with T, and stopping there (Lee 1998).

Procedure 2

Keep $\tau_{HG}=k\tau_{HT}$. For $0<k<1$ this would have the same net result as procedure 1.

An alternative continuous control procedure to consider is:

Procedure 3

Keep $d_{HG}=kd_{TG}$ (d_{HG}=distance HG, etc., and *k* is a constant). However, since this implies keeping $\dot{d}_{HG}=k\dot{d}_{TG}$, H would arrive at G moving at *k* times the speed of T (which ranged from 3 to 68 cm s^{-1}). The procedure would not therefore solve the task, which required that H stop at G. It may be argued, perhaps, that the procedure might be followed for most of the movement, with a different zeroing-in-on-the-goal procedure added at the end. However, that would leave unexplained how the zeroing-in-on-the-goal is controlled, which is explained by the τ-coupling procedures. Similar arguments apply against the hypothetical procedures of keeping $d_{HG}=kd_{HT}$ or $d_{HT}=kd_{TG}$.

Finally, the possibility of discrete control also needs to be considered:

Procedure 4

Move H ‘single shot’ to arrive at G at the same time as T; i.e., watch T, predict when it will reach G and then move H using only this timing information.

Materials and methods

Subjects

Six healthy human volunteers (two women and four men, aged 22–36 years) from the University of Minnesota academic environment participated as subjects. All were naive about the hypotheses behind the experiments. The experimental protocol was approved by the Institutional Review Board.

Procedure

The subject sat unrestrained in front of a 2D articulated manipulandum, which was oriented horizontally. The subject’s eyes were approximately 57 cm from a vertical 35.5-cm color monitor (Gateway 1024NI). By moving the manipulandum the subject controlled the position on the computer screen of a hand cursor (6-mm ring). The gain was set to unity so that the hand cursor moved the same distance as the manipulandum. The (*x, y*) screen coordinates of the hand cursor were digitally sampled at 100 Hz with a spatial resolution of 0.125 mm. The screen resolution was 640 pixels horizontally by 480 pixels vertically. The refresh rate was 60 Hz. A personal computer was used for experimental control, visual presentation and data collection.

The task is diagrammed in Fig. 1. The dotted lines are for graphical convenience and were not presented to the subject. To start a trial the subject first moved the hand cursor H until it was superimposed on a start zone (3 mm radius) located at bottom centre of the invisible triangle, 12.5 cm below the apex G. After this position had been maintained for a random period of 1–3 s, a target cursor T (6 mm radius) moved from the bottom along either the left or right side of the triangle up to the top G. The subject had to move the hand cursor H upwards from the start zone so that it stopped in a goal zone centred on G just as T arrived there. There were no constraints on the subject’s direction of movement. A trial was considered successful when the following conditions were met: (1) H was kept around the start zone until 100 ms after the target started to move (to prevent anticipatory movements); (2) H entered an invisible 6-mm-radius goal zone centred on G within 100 ms of T arriving at G; and (3) after entering the goal zone, H remained within 12 mm of the centre G of the zone for 0.5 s.

T was moved in the following 36 (3×6×2) different ways: at constant acceleration (starting at 3.0 cm s^{-1}), constant velocity, or constant deceleration (ending at 3.0 cm s^{-1}); with a motion time of 0.5, 0.8, 1.1, 1.4, 1.7, or 2.0 s; from the bottom left or the bottom right of the screen. Each experimental session consisted of 5 repetitions of the set of 36 conditions, presented in a randomised block design. No nesting was employed. Unsuccessful trials were re-randomised and repeated until correct performance was achieved.

Measuring the relative duration of τ-coupling

The relative duration of τ-coupling was measured as the percentage of data points lying in the ‘straight’ section of a graph (e.g., of τ_{HG} against τ_{HT}) terminating at the end of the hand movement. Emphasis was laid on analysing the latter part of the movement because that was the critical section for the task. The following algorithm was run on a computer. Considering a τ against τ plot to be of a time series (y_1, y_2,..., y_m) against another time series (x_1, x_2,..., x_m), the following sequence of computations was made, starting at the right-hand end of a plot, for n=10, 11, 12,... until the first data point (x_1, y_1) was reached: (1) a linear regression line was fitted to the rightmost *n* data points, i.e., to $\{y_{m-n+1}, y_{m-n+2},..., y_m\}$ against $\{x_{m-n+1}, x_{m-n+2},..., x_m\}$; (2) the standard deviation, S_n, of the points about the regression line (the standard error of estimate) was calculated. (3) The relative deviation, D_n, of the next data point, the ($m-n$)th point, from the regression line was calculated using the formula: D_n=[distance, measured in the *y*-direction, of the ($m-n$)th point from the regression line]/S_n. This procedure resulted in a set of values $\{D_n\}$, for n=10, 11,..., ($m-1$). Here D_n is the relative deviation of the *n*th data point, P_n, counting from the right, from the

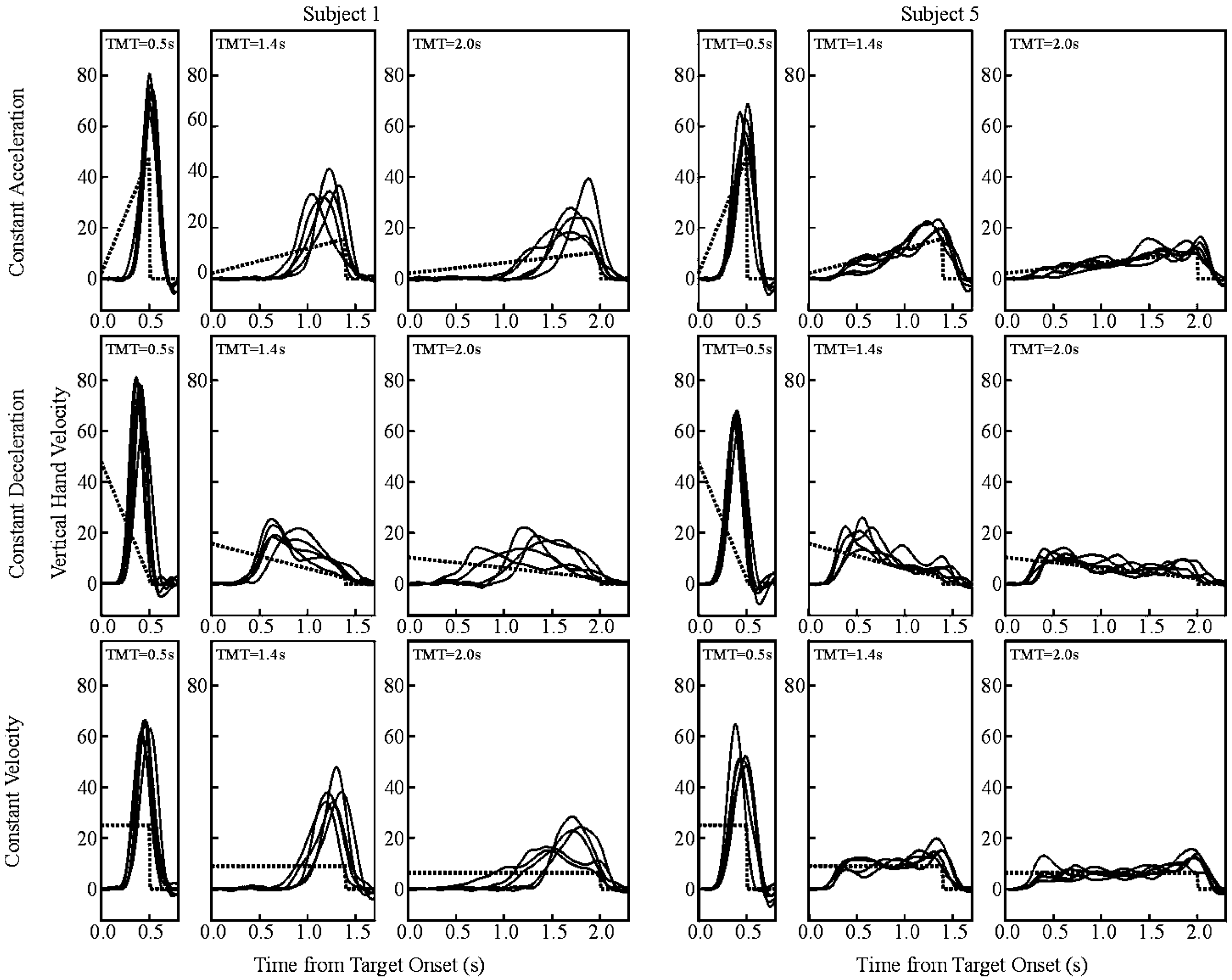


Fig. 2 Examples of velocity profiles of hand cursor H (Fig. 1) when executing the experimental task. Three of the six target motion times (*TMT*) are shown (*TMT*=0.5, 1.4, 2.0 s). *Top* Constant acceleration of target condition; *middle* constant deceleration condition; *bottom* constant velocity condition. Note that the velocity profiles are generally skewed differently across the three conditions, except for the short TMT of 0.5 s. How the skewness varied across conditions is shown in Fig. 3 (figure from Lee et al. 1997, Fig. 1)

linear regression line through the (n–1) data points to the right of P_n. Thus, when n is high (the leftmost points of each plot, see Fig. 4), the D_n value of a point is high because the leftmost points lie away from the straight-line trend of the rightmost points. Moving rightward along the τ against τ plot, D_n tends to decrease as the data points move more in line with the rightmost data points. The algorithm took the point when D_n first dropped to less than two as the start of the straight line of data points.

Results

Test of single shot hypothesis

If this hypothesis were correct, the velocity profile of the hand H should be the same whether the target T moved with constant acceleration, constant velocity or constant deceleration. However, the representative velocity profiles shown in Fig. 2 indicate this was not the case. In particular, the skewness of the velocity profile of the hand was found to systematically decrease across the three forms of motion of the target. Skewness was computed for each trial as the time from start to peak velocity of the hand H divided by its duration of motion. The start and end of motion of H were defined as the closest velocity zero-crossings preceding and following peak velocity. The mean skewness measures for each subject and each type of target motion are shown in Fig. 3. The type of target motion had a significant effect on skewness (F=12.742, P<0.0006). On the basis of these results we can say that this hypothesis is rejected. Hence we can conclude that the subjects controlled the motion of H online, and not in a single shot. This agrees with the findings from other studies (Georgopoulos et al. 1981; Milner and Ijaz 1990; Peper et al. 1994; Soechting and Lacquaniti 1983).

Test of τ-coupling hypotheses

Recall that hypothetical procedure 1 is to keep $\tau_{HG}=k\tau_{TG}$, and procedure 2 is to keep $\tau_{HG}=k\tau_{HT}$. For each trial we

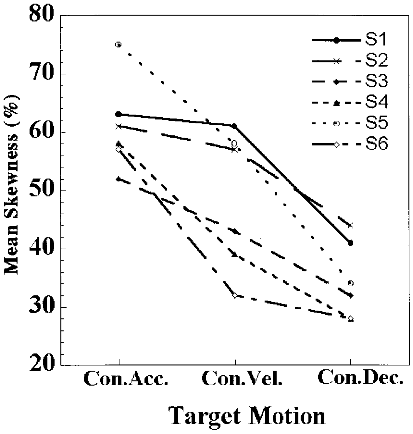


Fig. 3 Skewness of the velocity profile of the hand cursor H. This varied with the type of motion of the target T, indicating that the subjects were not controlling their movement as a 'single shot' but controlling it online

computed the graphs of τ_{HG} against τ_{TG} to test procedure 1 and the graphs of τ_{HG} against τ_{HT} to test procedure 2. Under each hypothetical procedure the respective graph should converge on a straight line through the origin. The graphs were computed from when the hand clearly started to move, defined as when its velocity reached 10% of its peak velocity on that trial, to when the velocity dropped to 10% of its peak velocity just before reaching G. This was to eliminate the noisy measurements of the velocity of the hand H at low values, because in calculating τ_{HG} the velocity of H appears in the denominator of the formula and so noisy estimates of the velocity are amplified in estimating τ_{HG}.

Regarding procedure 1, Fig. 4a, c, e presents representative data graphs illustrating how τ_{HG} and τ_{TG} changed over time for constant acceleration, constant velocity and constant deceleration targets. Figure 4g shows, for the same data, how τ_{HG} changed with τ_{TG}. As a comparison with procedure 1, Fig. 4b, d, f, h shows the data from the same experimental trials now plotted in terms of procedure 2 using the τ variables τ_{HG} and τ_{HT} instead of τ_{HG} and τ_{TG}. In Fig. 4h, each graph for procedure 2 tends smoothly and quite quickly to a straight line through the origin as time progresses, which indicates $\tau_{HG}=k\tau_{HT}$ coupling over most of the movement. The τ-coupling is also evident in Fig. 4b, d, f. In contrast, in Fig. 4g the graphs for procedure 1 converge less slowly toward linearity, indicating $\tau_{HG}=k\tau_{TG}$ coupling over less of the movement. This lesser degree of τ-coupling for procedure 1 compared with procedure 2 is also evident in Fig. 4a, c, e.

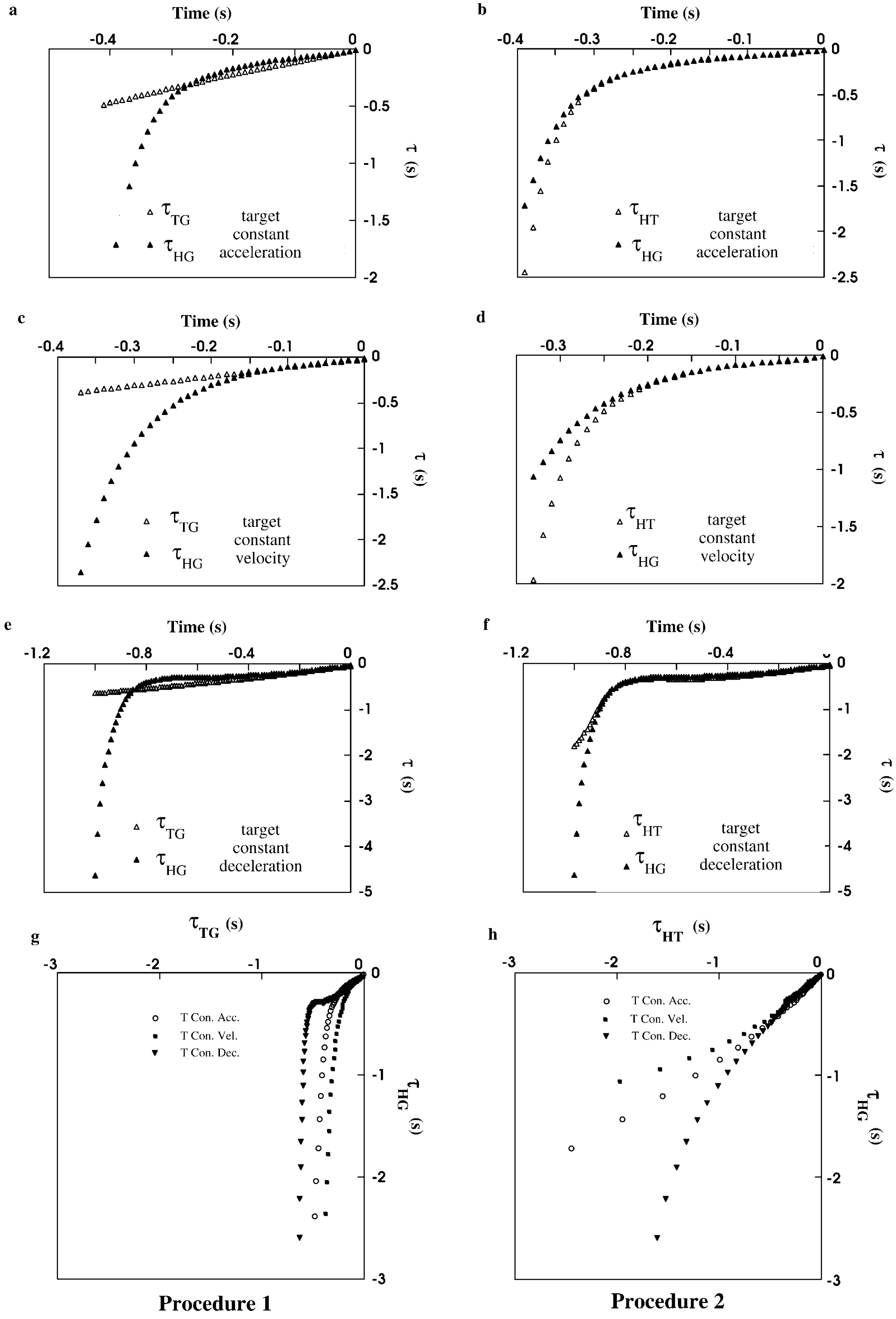
To measure the degree of τ-coupling evidenced in a data graph, we calculated the number of data points in the 'straight' section of the graph and the linear regression coefficients for that section, using a linear regression algorithm applied iteratively (see "Materials and methods"). The computer algorithm found the longest 'straight' set of consecutive data points terminating on the last point (corresponding to when the hand velocity reached 10% of its peak velocity – see preceding paragraph) and computed the r^2 of the linear regression line through the set and the number of points, *n*, in the set. Initial inspection of the data revealed a minority of trials in which the value of r^2 and/or *n* was atypically low. This was not unexpected since the subjects found the task very demanding and performance was poor on some trials. To avoid the values of r^2 and/or *n* on these trials distorting the majority picture, the set of data points found by the computer algorithm was accepted as a 'straight' set only if the r^2 of the linear regression line through the set was greater than 0.95 (i.e., the linear model accounted for 95% of the variance in the data) and the number of points in the set was greater than ten. Eighty percent of the τ_{HG} against τ_{HT} (procedure 2) plots and 62% of the τ_{HG} against τ_{TG} (procedure 1) plots met these criteria and were then further analysed, as described below.

Strength of τ-coupling

The strengths of the $\tau_{HG}=k\tau_{TG}$ τ-coupling (procedure 1) and the $\tau_{HG}=k\tau_{HT}$ τ-coupling (procedure 2) were measured, on each trial, by the r^2 values of the linear regressions through the 'straight' sections of, respectively, the τ_{HG} vs τ_{TG} plot and τ_{HG} vs τ_{HT} plot, as computed by the algorithm described above. r^2 lies in the range 0 to 1, with a value of 1 corresponding to perfect coupling. Figure 5a, c shows that the mean r^2 values were very high for both $\tau_{HG}=k\tau_{TG}$ coupling (procedure 1) and $\tau_{HG}=k\tau_{HT}$ coupling (procedure 2). Means (SD) of standard errors across subjects were low: 0.0029 (0.0007) for procedure 1 and 0.0024 (0.0004) for procedure 2. The procedure 2/procedure 1 ratios of mean r^2s across the six target motion times were, for subjects 1–6 respectively, 0.991/0.992, 0.987/0.985, 0.983/0.983, 0.984/0.978, 0.981/0.979, 0.981/0.980. All these values are significantly greater than the criterion value of r^2 of 0.95 used by the algorithm ($P<0.005$, *t*-test).

Relative duration of τ-coupling

This was measured, for each trial and for each type of τ-coupling ($\tau_{HG}=k\tau_{TG}$ and $\tau_{HG}=k\tau_{HT}$), as the percentage of the movement time of H that corresponded to the 'straight' section of the τ_{HG} vs τ_{TG} plot or the τ_{HG} vs τ_{HT} plot, as determined by the iterative regression algorithm described above. It was assumed that the higher the relative duration of τ-coupling the stronger the evidence for τ-coupling. Figure 5d, b shows that the mean relative duration of $\tau_{HG}=k\tau_{HT}$ coupling (procedure 2) was generally higher than that of $\tau_{HG}=k\tau_{TG}$ coupling (procedure 1). Means (SD) of standard errors across subjects were low: 4.4 (0.44) for procedure 1 and 4.6 (1.10) for procedure 2. The procedure 2/procedure 1 ratios of the relative durations of τ-coupling averaged across the six target motion times were, for subjects 1–6 respectively, $71/41^{+++}$,


a
Time (s)
-0.4
-0.2
0
-0.5
-1
-1.5
-2
τ (s)
τ_{TG}
τ_{HG}
target constant acceleration
b
Time (s)
-0.4
-0.3
-0.2
-0.1
0
-0.5
-1
-1.5
-2
-2.5
τ (s)
τ_{HT}
τ_{HG}
target constant acceleration
c
Time (s)
-0.4
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-0.2
-0.1
0
-0.5
-1
-1.5
-2
-2.5
τ (s)
τ_{TG}
τ_{HG}
target constant velocity
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Time (s)
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-0.1
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τ (s)
τ_{HT}
τ_{HG}
target constant velocity
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Time (s)
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τ (s)
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τ_{HG}
target constant deceleration
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Time (s)
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Procedure 1
Procedure 2

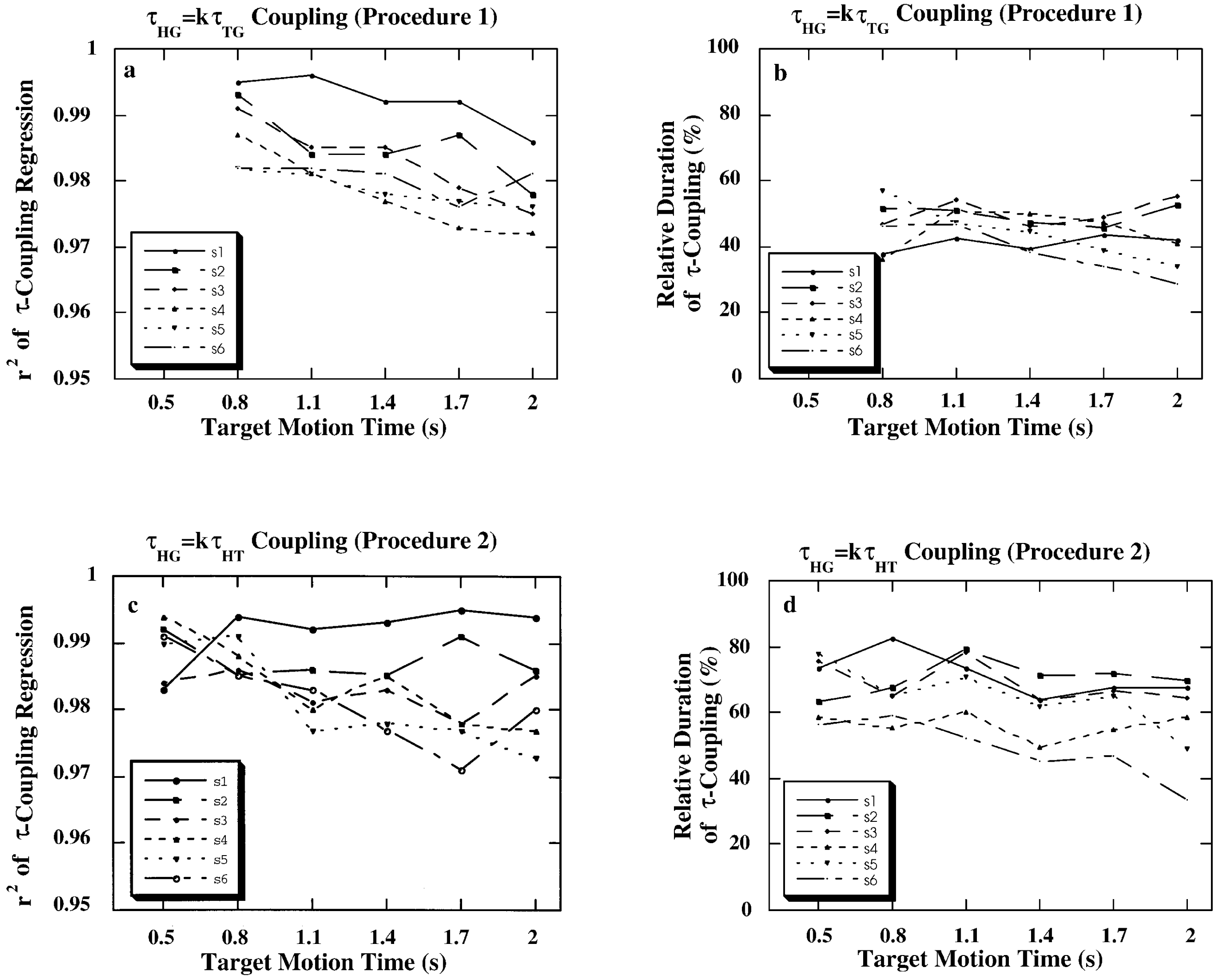

Fig. 5a–d *Top* Measures of $\tau_{HG}=k\tau_{TG}$ coupling (procedure 1). *Bottom* Measures of $\tau_{HG}=k\tau_{HT}$ coupling (procedure 2). Means are plotted for each subject and each target motion time. **a, c** r^2 of the τ-coupling linear regressions ($r^2=1$ if coupling perfect). **b, d** Relative duration of τ-coupling (the percentage of the hand movement time when the hand was τ-coupled). Taken together, the results indicate that the subjects guided contact by $\tau_{HG}=k\tau_{HT}$ coupling (procedure 2)

◀ **Fig. 4** Representative data graphs illustrating how $\tau_{HG}=k\tau_{TG}$ (procedure 1) and $\tau_{HG}=k\tau_{HT}$ (procedure 2) changed together over time for constant acceleration **(a, b)**, constant velocity **(c, d)** and constant deceleration **(e, f)** targets. **g** and **h** show respectively, for the same data, how τ_{HG} changed with τ_{TG} (procedure 1) and how τ_{HG} changed with τ_{HT} (procedure 2). Note that in **h**, each graph tends smoothly and quite quickly to a straight line through the origin as time progresses, which indicates $\tau_{HG}=k\tau_{HT}$ coupling (procedure 2) over most of the movement. On the other hand, in **g** the graphs for procedure 1 converge less slowly toward linearity, indicating $\tau_{HG}=k\tau_{TG}$ coupling over less of the movement. This higher degree of τ-coupling for procedure 2 than for procedure 1 is also evident in comparing **b** and **a**, **d** and **c**, and **f** and **e**

70/50^{+++}, 69/50^{+++}, 56/45^{+++}, 65/44^{+}, 49/39^{+} (where $^{+}$ and $^{+++}$ mean that the relative duration for procedure 2 was significantly greater than for procedure 1 at $P<0.05$ and $P<0.005$, respectively, one-tailed *t*-test). Thus the relative duration of τ-coupling more strongly supports, for all subjects, the use of $\tau_{HG}=k\tau_{HT}$ coupling (procedure 2) as against $\tau_{HG}=k\tau_{TG}$ coupling (procedure 1).

Discussion

Controlling contact with moving or stationary objects or surfaces is a necessary skill for all animals. It requires sensorily guiding the closure of gaps between effectors (hands, feet, etc.) and destinations. We investigated a demanding form of this sensorily guided skill in a task run on a computer monitor (Fig. 1). Subjects had to move an effector (a cursor, H) to a goal zone G so that H stopped at G just as a moving object (a cursor T), moving in a straight line in various ways, reached G. Thus the task was similar to reaching to trap a moving ball under the hand at a particular place.

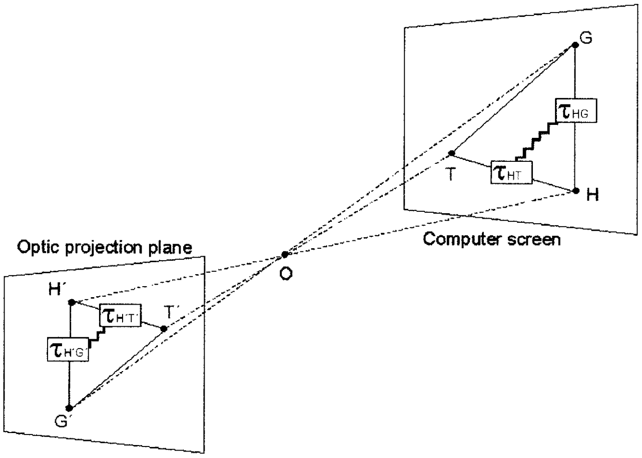

Fig. 6 This figure shows how the τ-coupling $\tau_{HG}=k\tau_{HT}$ (procedure 2) could be optically specified. Points H, T and G optically project into image points H′, T′ and G′ on the parallel optic projection plane (model retina). From similar triangles, $d_{HG}=Cd_{H'G'}$ and $d_{HT}=Cd_{H'T'}$, where d is distance and C is a constant. Differentiating with respect to time, $\dot{d}_{HG}=C\dot{d}_{H'G'}$ and $\dot{d}_{HT}=C\dot{d}_{H'T'}$. Dividing corresponding equations yields $d_{HG}/\dot{d}_{HG}=d_{H'G'}/\dot{d}_{H'G'}$ and $d_{HT}/\dot{d}_{HT}=d_{H'T'}/\dot{d}_{H'T'}$. That is, $\tau_{HG}=\tau_{H'G'}$ and $\tau_{HT}=\tau_{H'T'}$. Thus, maintaining the optical τ-coupling $\tau_{H'G'}=k\tau_{H'T'}$ (for a constant k) would ensure that the motion-gap τ-coupling $\tau_{HG}=k\tau_{HT}$ also was maintained

Of the four hypothetical procedures tested, the results most supported the hypothesis that the movement of the effector H was guided by τ-coupling the τs of the HG and HT gaps, τ_{HG} and τ_{HT}, i.e., by keeping $\tau_{HG}=k\tau_{HT}$, where k is constant during the movement (procedure 2). The data less strongly supported $\tau_{HG}=k\tau_{TG}$ coupling (procedure 1) insofar as the relative duration of this type of τ-coupling was lower. The apparent, albeit weaker, support for the $\tau_{HG}=k\tau_{TG}$ coupling (procedure 1) is probably due to the three τs – τ_{HG}, τ_{TG}, τ_{HT} – being correlated to a certain degree, particularly when H and T are getting near G. Thus, the earlier-starting $\tau_{HG}=k\tau_{HT}$ coupling (procedure 2) would, as time progressed, generate an apparent $\tau_{HG}=k\tau_{TG}$ coupling (procedure 1). The argument is, of course, not reversible: a later-starting $\tau_{HG}=k\tau_{TG}$ coupling (procedure 1) could not generate an apparent *earlier*-starting $\tau_{HG}=k\tau_{HT}$ coupling (procedure 2). Thus it is reasonable to argue that the data present a stronger case for $\tau_{HG}=k\tau_{HT}$ coupling (procedure 2).

Solving the experimental task by $\tau_{HG}=k\tau_{HT}$ coupling makes sense for two reasons. First, if the coupling $\tau_{HG}=k\tau_{HT}$ were maintained, then it follows mathematically that H would reach G at low velocity at the same time as it reached T no matter how the speed of T might vary (see Lee 1998, p. 246 for proof). This was what the task demanded. Thus, maintaining $\tau_{HG}=k\tau_{HT}$ coupling would be a simple and rigorous procedure for prospectively guiding H to T and simultaneously to G.

Second, as shown in Fig. 6, the values of τ_{HG} and τ_{HT} are each specified straightforwardly in the optic array at the subject's eye by the values of the corresponding optical τs: i.e., $\tau_{HG}=\tau_{H'G'}$ and $\tau_{HT}=\tau_{H'T'}$, where H′, G′ and T′ are the optic images of H, G and T. Thus the values of τ_{HG} and τ_{HT} could be registered directly in the brain, via $\tau_{H'G'}$ and $\tau_{H'T'}$. Neural activity corresponding to optically specified τ has been found in both locust and pigeon brain (Rind and Simmons 1999; Sun and Frost 1998). Therefore τ_{HG} and τ_{HT} could be coupled by moving H so that the neural activities corresponding to $\tau_{H'G'}$ and $\tau_{H'T'}$ stay in constant ratio. In contrast, the gap sizes, velocities and accelerations are not straightforwardly specified optically. For example, the distance between H and G on the computer screen does not equal the distance between the optic projections of H and G at the eye (Fig. 6) and would likely require more neural processing than τ_{HG}.

Direct sensory specification of τ of a motion gap is not confined to vision but, in principle, applies to any sensory input variable (e.g., acoustic, mechanical or electric) that is a power function of the size of the motion gap (Lee 1998). Bats, for example, could sense τ through echolocation.

All this is not to suggest that there is but one type of τ-coupling involved in controlling contact. Different forms of τ-coupling are evident in other skills. For example, analysis of the flight trajectories of bats landing on a perch using echolocation (Lee et al. 1995) indicated that they τ-coupled the τ of the current distance gap, r, between bat and perch, and the τ of the angular gap, α, between the current direction to the perch and the direction aimed at for the final approach (which experiment showed to be consistent to within ±4°). In another study, movement of the hand was analysed in adult human subjects raising morsels of food to the mouth with eyes closed (Lee et al. 1999). Interestingly, the basic control geometry was found to be the same as for the bat flying to the perch: the results again evidenced $\tau_\alpha=k\tau_r$ coupling with r now representing the hand-mouth gap and α the angular gap between the hand-mouth line and its goal-direction at final approach. In this case, mechanoreceptor information was apparently used to control the closure of the gaps, rather than acoustic information, as used by the echolocating bat. Evidence for precocious τ-coupling has been found in the control of suction by newborn babies when bottle-feeding (Craig and Lee 1999).

τ-coupling may also guide an effector so that it makes contact with an object or surface with a required force. Evidence for this comes from a recent study of precision putting in golf, which indicated that τ-coupling (in a different form than in the present experiment) was involved in controlling the distance the ball was hit (Craig et al. 2000). Thus it seems that τ-coupling may be generally implicated in guiding different aspects of controlled contact.

Conclusions

The present and related experiments suggest that τ-coupling may be a basic principle used by different species in sensorily guiding contact with objects and surfaces. τ-coupling may be between τs of gaps of the same or different dimensions (e.g. distance and angle), and the τs might be sensed in different ways through, for example, the eyes, ears or mechanoreceptors. τ-coupling provides a simple, reliable and robust means of synchronising the closure of two or more gaps between effectors and goals, and regulating the dynamics of closure of the gaps, both of which are necessary in generating coordinated purposeful movement.

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