

Review

Obtaining information by dynamic (effortful) touching

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Dynamic touching is effortful touching. It entails deformation of muscles and fascia and activation of the embedded mechanoreceptors, as when an object is supported and moved by the body. It is realized as exploratory activities that can vary widely in spatial and temporal extents (a momentary heft, an extended walk). Research has revealed the potential of dynamic touching for obtaining nonvisual information about the body (e.g. limb orientation), attachments to the body (e.g. an object's height and width) and the relation of the body both to attachments (e.g. hand's location on a grasped object) and surrounding surfaces (e.g. places and their distances). Invariants over the exploratory activity (e.g. moments of a wielded object's mass distribution) seem to ground this 'information about'. The conception of a haptic medium as a nested tensegrity structure has been proposed to express the obtained information realized by myofascia deformation, by its invariants and transformations. The tensegrity proposal rationalizes the relative indifference of dynamic touch to the site of mechanical contact (hand, foot, torso or probe) and the overtness of exploratory activity. It also provides a framework for dynamic touching's fractal nature, and the finding that its degree of fractality may matter to its accomplishments.

Keywords: exploratory activity; information about; invariants; tensegrity; fractality

1. INTRODUCTION

Information understood ecologically is a special kind of resource—a resource about the nature and whereabouts of other resources understood as opportunities for action (i.e. affordances) that further biological processes [1]. Information understood ecologically is a physical feature of the environment consisting of special patterns in ambient energy distributions that are specific to the environment taken with reference to the organism [2-4]. This *information about* enables an organism to encounter its surroundings, to regulate its encounters and to be aware of its activities [1]. 'Aware of' entails neither consciousness nor declarative knowledge. What it does entail is perceptually based capacities for meaningful discrimination and actions organized by those discriminations. However limited and specific 'aware of' might be, it is, arguably, characteristic of all organisms, of all 96 phyla in the kingdoms of Bacteria, Protoctista, Animalia, Fungi and Plantae [5].

Information may be imposed or obtained; we focus on obtained information, presenting arguments primarily from humans. Touching, together with smelling, tasting, listening and looking, are modes of exploratory activity that facilitate the obtaining of information [2].

2. PREVIEW

We begin with a brief exposition of the nature of dynamic touching, giving emphasis to (i) information in Gibson's [2,3] law-based sense, (ii) tensegrity as a hypothesis about how a body's deformable tissue can function as a medium for law-based information, and (iii) 'outness' as a classical problem resolvable by (i) and (ii). This is followed by summaries of research (both old and new) on the properties of grasped or held objects that are selectively perceptible by dynamic touching, whether by free wielding (swinging, shaking, twisting) or mere supporting, and on the similarities between perceiving attached objects and perceiving segments of the body. These summaries identify primary characterizations, conceptions, experimental methods and metrics (e.g. mass moments, the spinor theory of rotations, affordances, metamers, recurrence and fractal analyses) and set the stage for extending dynamic touching to the registering of distances travelled by legged locomotion and the learning of, and orienting to, places. We conclude with examples of how and why experiments on dynamic touching by humans can and should provide insight into the active tactile capabilities of other animals.

3. NATURE OF DYNAMIC TOUCHING

Effortful or dynamic touching is a kind of touching that is based on the deformation of muscles and allied connective tissue, as when an object is supported and moved by the body. It is manifested through very many kinds of exploratory activities. An incomplete list

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One contribution of 18 to a Theo Murphy Meeting Issue 'Active touch sensing'.

for humans includes holding, wielding, lifting, carrying, pushing, pulling, prodding, groping, bending, stretching, tugging, folding, twisting, squeezing, chewing and walking. As will become evident, by dynamic touching, humans can perceive the body (proprioperception), attachments to the body (exteroperception), the relation of the body to attached objects and surrounding surfaces (pro-exteroperception) and the relation of attached objects and surrounding surfaces to the body (ex-proprioperception) [6].

Dynamic touching is a subsystem of the haptic perceptual system [2]: the system by which one perceives the body, attachments to the body and surfaces adjacent to the body, by means of the body. Within the ecological approach to perception and action, 'perceptual systems' are distinguished from 'senses'. The enduring seventeenth-century doctrines that the senses are mere conveyors of sensory quality and the means for obtaining knowledge are contradictory. To be the latter, they cannot be the former. In the ecological perspective, perceptual systems are active means for detecting 'information about' (in the sense of specificity to). To elaborate on remarks above, it is a law-based definition of information-patterned energy distributions (e.g. scattered light, fronts and trains of pressure waves, diffusing volatiles) specific to their sources (e.g. surface layout, mechanical disturbances, chemical events). It stands in sharp contrast to the commonplace allusions to information as neural signals and/or Shannon information and/or cues or clues. Vortex flows in water are specific to functionally meaningful aspects of their sources (e.g. particular movements of a particular kind of organism) by virtue of the laws of hydrodynamics [7]. Harbour seals detect this 'information about' by means of their mystacial vibrissae [8]. They detect it by dynamic touch.

(a) A medium for dynamic touching?

In the preceding example, information in the specificational sense is carried in the spatio-temporal patterning of a medium, namely water. In respect to dynamic touching of attachments to the body, the information can only be defined over the spatio-temporal patterning of the body's tissues. This raises the questions of whether deformable tissues comprise a medium for dynamic touching, and if so, how should it be defined [9].

There are reasons to suppose that the vertebrate body and, perhaps, the invertebrate body [10], are organized as tensegrity structures [11]. Tensegrity structures are unique mechanical systems that derive their support function and mechanical stability from continuous tension and local intermittent compression. In the specific case of vertebrates, the tensegrity system is multimodular and probably complex in the sense of no identified constitutive tensegrity structure [12]. It is, in all probability, an assemblage of different typologies and formal classes of tensegrity subsystems [12,13] nested from level to level. Identifying the system begins with identifying the level-dependent compression and tension elements.

At the level of the body, the bones can be thought of as the compression members, which are embedded in and balanced by the tightly interconnected soft tissue (myofascia) network that constitutes the tension-bearing structures. At the cellular level (which includes receptors), the internal microtubule struts and extracellular matrix adhesions can be thought of as the compression members, which are embedded in and balanced by the tightly interconnected network of cytoskeletal microfilaments and intermediate filaments that constitute the tension-bearing structures.

A tensegrity system is constantly in balance with its external and internal force environments. Such force balance is guaranteed by a baseline level of tension, or pre-stress, established over the tension-bearing elements. Pre-stress removes any slack in the system and makes it immediately responsive to mechanical stress; consequently, a force applied locally can potentially be sensed globally [11]. As a result of pre-stress, activities occurring locally in multiple parts and at multiple levels of the system coordinate naturally to re-establish a force balance should it be disturbed by mechanical forces within and adjacent to the system. Thanks to this force-balance constraint, the global deformations of a tensegrity structure relate systematically to the mechanical forces impressed upon it.

Although multiple mechanoreceptors are active at multiple locations during dynamic touching, rapid compression to a few degrees of freedom would be possible in principle with the force-balance property allowed by a biotensegrity architectural organization. As a result, tension distributions and their changes (owing to internal or external forces) may be registered at the level of the body as a unit [14]. At issue then for dynamic touching of an object attached to the body is whether the invariants of the tension distributions would be information about the object's properties.

(b) The outness problem

To enhance appreciation of dynamic touching and the need to focus upon the challenges of 'information about' consider that when a person touches an object with a hand-held stick (and presumably when a whip spider or a crayfish touches an object with its secondary antenna), the object is perceived to be at the end of the probe rather than at the site of the probe's attachment to the body, or in the head. For philosophers and psychologists over the centuries, this is the 'outness problem': How can sensations and perceptions, located in a sensory organ, or in the mind, be projected out into the environment? The problem is actually worse. There are two contemporaneous outness problems when contacting an object with a stick. The length of the stick and the distance to the object that the stick touches are independently perceptible [15]. For phyla that obtain information by touching, the proper and leading question is how could the play of forces on muscles and connective tissue, arising from movements of the body and contact-engendered forces engender awareness of the environment being probed and the attachment to the body with which it is being probed?

4. WHAT PROPERTIES OF HAND-HELD OBJECTS ARE DYNAMICALLY TOUCHABLE, AND HOW?

In their original experiments, Solomon & Turvey [16] showed that by wielding a uniformly dense rod grasped at one end, a person could obtain a non-visual



Figure 1. (a) In a typical experiment, an object is wielded out of view and perceived properties such as height and width are indicated via magnitude production. (b) Perceived properties are in the scale of actual properties. (c) Different properties are constrained by different invariants of the mass distribution (light grey bars, width; dark grey bars, height).

impression of the rod's length that was within a marginal tolerance of its actual length. As a general rule, the scaling of extents perceived by dynamic touching to actual extents is neither absolute (a perfect match) nor relative (right order but arbitrary values). As Bingham [17] noted, when judgements are within a marginal tolerance of the actual values, it must be assumed that there is information available that is more definite than the information supporting relative scaling. He called this type of scaling—the type that seems to characterize perception by dynamic touch—'definite'.

Most research on dynamic touching has been founded on the hypothesis that the definite scaling of the non-visual perceptions of spatial dimensions (and other properties) of a wielded object has its basis in the moments of the object's mass distribution. The three moments, namely the zeroth (mass), first (static moment) and second (moment of inertia), are invariant over the variations in the forces brought to bear on the objects and on the body's tissues, and variations in the motions of the objects and the deformations of the tissues during wielding. Following Solomon [18], a major emphasis has been given to the tensor of inertia, particularly in respect to the three principal moments (eigenvalues) and three principal directions (eigenvectors) that yield the tensor's geometric configuration, the inertia ellipsoid.

(a) A representative experiment

Investigations of the dynamic touching of spatial and other properties of firmly grasped and manually wielded rigid objects hidden from view have involved experimental objects that have varied (both within experiments and over experiments) in shape, size, material composition and uniformity of density [19]. Additionally, in most experiments, participants have received minimal training, just enough to acquaint them with the task.

For the representative experiment depicted in figure 1*a* ([20], experiment 1), the objects were three sets of three rectangular wooden blocks, one block for each of the relations: height > width, height = width, height < width. Across the sets, the mass differed (approx. 0.39, 0.89 and 1.67 kg). Each of the nine objects was wielded by means of a handle of the same mass, length and radius. On a trial, participants wielded first for one dimension (say, height) and then for the

other (width) and reported their perceptions by magnitude production. In the mean, participants judged objects as being higher than they were wide when that was the case, as being wider than they were high when that was the case and as being equal in height and width when that was the case. Further, participants' height and width perceptions were (i) within the range of the objects' actual dimensions in the absence of foreknowledge of that range and with the opportunity to report heights and widths up to approximately 1 m (figure 1b), and (ii) differentially correlated with the largest (I_1) and smallest (I_3) principal moments of inertia (figure 1c).

(b) Perceiving properties of a hand-rod system

Given an instruction to perceive by dynamic touching the property P_i , a person seemingly instantiates the function $P_i = h_i$ (moments).

That is, the mechanoreceptors and the attendant neural and fascia nets can be conceptualized as implementing a haptic function (h_i) on the mass moments that delivers the perception (of P_i) requested by the experimenter and, thereby, intended by the cooperative participant. Adopting this conceptualization of dynamic touch can lead to a deeper appreciation of the abstractness of this haptic subsystem's capabilities, and the variables to which it is sensitive. The strategy adopted by investigators of dynamic touching is that of identifying the various h_i . For hand-held rods, evidence to date (see [21,22] for reviews) suggests different h_i for the following P_i : whole rod length, partial rod length (fore or aft of the hand at an intermediate grasp location on the rod), centre of percussion, location of grasp and orientation to hand (determined by a bar perpendicular to the rod's longitudinal axis).

Perceptions of these properties have been determined to be perceptually independent (e.g. the perception of rod length does not depend upon the perception of grip position, and vice versa). Demonstrating perceptual independence involves a series of statistical analyses, the culmination of which is the conclusion that the joint distribution of two perceptual responses either is or is not equal to the product of the distributions of each perceptual response alone [23,24]. In the first case, the perceptual responses are statistically independent; in the second case, they are not. (For a summary, see [21].)



Figure 2. (a) With wielding from the centre of the rod, conditions A, B and C are created, respectively, with no added mass, and with mass behind or in front of the grasp. (b) The pattern of perceived lengths depends on the intention to perceive whole or partial length. The pattern is as would be expected if perceivers could fractionate the moment of inertia.

Observations such as the preceding suggest that, collectively, the mechanoreceptors and the attendant neural and fascia nets are organized as smart perceptual instruments [25]: they capitalize on invariants, they abide single-valued functions, they yield definitely scaled measures and they are softly assembled. The latter is in reference to observations suggesting that any given haptic instrument can be assembled over different anatomical structures and that different haptic instruments can be assembled over the same anatomical structure [22].

5. SELECTIVELY ATTENDING TO WHOLES (EXTEROCEPTION) AND TO PARTS RELATIVE TO GRASP (EXPROPRIOCEPTION)

Solomon and colleagues [16,26] found that when a rod is manually grasped at some point along its length, a person could, on instruction, attend to the rod's whole length or a partial length (for example, the length of the rod forward from the hand). This selective ability has been most studied through the experimental manipulations schematized in figure 2. For the three mass conditions depicted in figure 2, with point of grasp at the rod's midpoint, the whole length of stimulus A should be perceived as shorter than B and C, which, in turn, should be perceived to be equal in length. The attached mass makes the moment of inertia of stimuli B and C equivalent and greater than stimulus A. Now consider the perception of partial length for the same three mass conditions. If partial length forward of midpoint is perceptually isolable in a way that is functionally equivalent to cutting off the rearward portion of the rod, then stimuli A and B should be perceived as equal in length (same moment of inertia if the attachment point is treated as the endpoint) and shorter than stimulus C (greater moment of inertia if the attachment point is treated as the endpoint).

The upper limbs (rods grasped in a hand) and lower limbs (rods attached to a foot perpendicular to the leg's longitudinal axis) have passed these tests of part-whole selectivity [27], as has the body as a whole (rods attached horizontally to the shoulders, centred about the first cervical vertebra) [28]. For the whole body case, the touching was achieved primarily through axial rotations, flexions-extensions and lateral bending of the trunk—motions similar to those of dynamic touching of rods grasped in a hand or attached to a foot.

That selective dynamic touching of attachments to the body proves to be indifferent to the attachment site might be expected from the tensegrity hypothesis. Dynamic touching by any part of the body entails muscular effort, and muscular effort entails time-varying deformation of muscles and connective tissues, which in turn entails collective stimulation of the embedded mechanoreceptors. The sensory resolution at the particular point of attachment of the object to the body is irrelevant because any muscular effort engenders non-local stimulation.

(a) The theoretical challenge of part-whole perception

The fractionation of the mass distribution, the separating of the part from the whole, is not analogous to physically cutting off the unattended part; the selective perception of the part is constrained by the mass distribution of the whole [29,30]. Experiments using a methodology somewhat more elaborate than that depicted in figure 2 reveals the theoretical challenge of understanding selective dynamic touch.

In these experiments, participants wielded rods grasped at their midpoints with attachments of either 50 or 100 g on either side of the hand, and were asked to report length on one side or the other of the hand ([31]; see also [32]). Three facts are of relevance. First, the perceived length of a given rod segment did not differ as a function of its direction from the hand. Second, the perceived length of the weighted rod segment exceeded that for the non-weighted rod segment. Third, the perceived length of the non-weighted rod segment was identical for the two mass variants whereas the perceived length of the weighted rod segment was longer for the larger mass variant (100 g).

To accommodate this complicated but reliable pattern of results, Turvey and colleagues have pursued a strategy of supplementing the tensor of inertia with the attitude spinor from the spinor theory of mechanical rotations advanced by Hestenes [33,34]. The attitude spinor represents two equivalent rotations (of the inertia ellipsoid relative to the reference frame of the hand) with opposite orientations or senses. It allows the conjecture that the principle determining the above pattern of results is selectively attending to one of the two senses of rotation. Adopting this conjecture accommodates the data (for elaboration, see [21,22,35]). Whether this spinor-supplemented inertia tensor theory is the right theory and whether any theory of dynamic touching limited to second moment conceptions (that is, ignoring zeroth and first moment conceptions) is sufficient are open issues awaiting more research [30,36,37].

6. WHEN OBJECTS ARE MERELY SUPPORTED

Dynamically touching the length of a hand-held rod can occur in the absence of explicit movement of the rod [38]. The conventional definite scaling is found, and the mean, accuracy and reliability measures can



Figure 3. The length of a rod that is held still is perceived whether the contact is distributed across (a) the palm of one hand, (b) the bottom of one hand and the top of the other, (c) the bottom of a hand and the top of a knee, (d) the bottom of a hand and an environmental support, or (e) the top of a hand and an environmental support.

be comparable for the two kinds of touching, that is, with and without intentional exploratory activity ([39], experiments 1 and 2).

There is one especially interesting variant of dynamic touching by mere supporting (alias, static holding) [40]). It is depicted in figure 3. In each of five rod-support situations, a given occluded rod was held horizontally, on one side of its centre of mass, with one upward (U) and one downward (D) force. Perceived rod length satisfied definite scaling in each of the five situations, that is, when D and U were distributed over the surfaces of one hand, two hands and a hand and a knee, and when only D or only U was provided anatomically, the other being provided by an environmental support. For rods of lengths 76, 91, 107 and 122 cm (and mass 66, 76, 86 and 91 g), mean perceived lengths of 12 participants over situations (figure 3a-c) were 74.38, 91.83, 105.96 and 114.00 cm, with no interaction between rod length and rod-support situation. For the same rods, and for a different group of 12 participants, mean perceived lengths over situations (figure 3b,d,e) were 75.07, 95.63, 109.45 and 122.68 cm, again, with no interaction between rod length and rod-support situation. The non-interaction underscores the indifference of perception by dynamic touching to anatomical and neural details. Other experiments within the same series make the same point. Perceived length decreased as the distance between D and U increased, a manipulation that reduced the first and second moments. The decrease occurred in the same degree when both D and U were provided anatomically (figure 3a-c) and when only one was provided anatomically (figure $3d_{e}$).

(a) The issue of minimal exploratory activity

Supporting an object with the goal of perceiving a prescribed property is not a case of zero exploratory activity. It is a case of minimal exploratory activity, intentionally constrained, but not purposely conducted. Minimal exploratory activity is in the form of fluctuations.

In respect to wielding, subtle intent-specific variations have been investigated [41] using recurrence quantification analyses (RQA; [42]), a nonlinear method for identifying and characterizing subtle repeating patterns (i.e. time correlations) in data that may be irregular and non-stationary. Systematic differences in RQA measures were found when wielding under the different intentions of 'perceive width' and 'perceive height' (e.g. figure 1*a*), and under the different intentions of 'perceive rod length in front of the hand' and 'perceive the hand's position on the rod' (as can be done in a variant of the task depicted in figure 2a).

RQA measures and similar measures of variability enrich the conception of exploratory procedures (EPs) advanced by Lederman & Klatzky [43]. They promise quantification, within any given setting, of an EP's complexity, determinism and stability [41]. In this respect, detrended fluctuation analysis (DFA; cf. [44]) and growth curve modelling (GCM; cf. [45]) applied to the EP of wielding suggest that its fluctuations distribute scale invariantly, consistent with fluctuations in fractal systems generally, and that perception by means of this EP depends on the degree to which it is fractal [46]. As Stephen et al. note, an implication of their findings is that dynamic touching by wielding is driven, perhaps fundamentally so, by interactions-that the perception of the properties of wielded objects is an emergent outcome of interactions across time scales, a notion compatible with the tensegrity conception of the haptic medium.

Returning to the issue of dynamic touching by merely supporting (figure 3), the parallels between perception by supporting and perception by free wielding suggest that structured fluctuations may be common to both. As a first step to addressing this possibility, a wholebody variant of the partial rod length versus the whole rod length paradigm has been adapted (figure 2). Experiments similar to that of Palatinus et al. ([28]; see above) are currently being conducted without intended movement, with participants quietly standing on a force platform. A first and essential observation is that the canonical partial report-whole report pattern (that shown in figure 2b) replicates in the absence of overt body movements. Given this observation, inquiry is now being directed to the motion of the body's centre of pressure (COP): Are the COP fluctuations fractal? If so, do the partial and whole perceptions depend on the degree of COP fractality? Applications of DFA and GCM to the COP data obtained to date suggest that the answer may be 'yes' to both questions.



Figure 4. (a) Masses can be positioned on tensor objects to bring about different resistances to rotational acceleration in different directions with consequences for heaviness (despite sameness in zeroth and first moments, the lower object is perceived 'heavier' [49]); (b) within a heaviness or moveableness space, combinations of mass, inertia ellipsoid symmetry and inertia ellipsoid volume yield metameric planes; (c) metamers for perceived moveableness are not metamers for perceived length (unfilled bars, 374 g; filled bars, 534 g).

7. METAMERS AND AFFORDANCES

An object can be moved in a variety of ways. Transporting it, for example, as opposed to using it as a probe requires the availability of information about that object as it relates to those activities. Given a particular object grasped in a particular way, how much force is needed and how should it be directed in order to move the object? How much force is needed and how should it be directed in order to reach out with that object? The behavioural possibilities of an object are its affordances [47].

When an object is grasped and manipulated, tissue deformation is tied to the mass distribution of the object. Special experimental objects allow direct control of the mass distribution and, thereby, movement-relevant information. So-called tensor objects ([48]; figure 4a) employ a stem with crossbars whose positions along the stem can be adjusted. In addition, masses can be attached to the crossbars at positions close to or far from the stem. With the crossbars at one end of the stem and the grasping hand at the other, the object has large magnitudes of the principal moments or eigenvalues I_1 and I_2 . With the crossbars brought close to the grasping hand, I_1 and I_2 are much less. Similarly, if the attached masses are far from the stem, the object is more difficult to twist than if they are close to the stem; the principal moment I_3 is larger or smaller, respectively.

These manipulations of a tensor object are independent of each other, and can be rendered on an object of fixed mass (the total mass of the branches and attachments), fixed geometry (the extents of the stem and branches) and fixed first moment. Of course, the sizes of the attached masses can be increased, thereby increasing the mass of the tensor objects, but their judicious placement can result in the same eigenvalues as lighter objects. In other words, tensor objects can be configured to have a fixed mass with different eigenvalues or the same eigenvalues for different masses.

The eigenvalues define a geometric characterization of the inertia tensor, the *inertia ellipsoid*, which provides two movement-relevant quantities. The ellipsoid volume, given by $V = 4/3 (I_1 \times I_2 \times I_3)^{1/2}$, is related to the amount of torque needed to move the object. The ellipsoid symmetry, given by $S = 2I_3/(I_1 + I_2)$, is related to how that torque should be directed. Particular combinations of mass M, S and V define distinct planes in what might be understood as a 'moveableness' space (figure 4b). In experiments with objects configured as in the foregoing, magnitude estimation is used to report how heavy the object feels or, alternatively, how movable it feels. A standard object is designated '100' and test objects are evaluated relative to that. Objects from a single MSV plane are perceived as equally heavy or equally movable—they are metamers; they are perceived as different from objects from a different metameric plane (figure 4c, upper). Importantly, if those same objects are judged for length, they are no longer metameric (figure 4c, lower) [49].

8. DYNAMICALLY TOUCHING LIMB POSTURE

The principles of dynamically touching attached objects ought to apply to the limbs. The arm, for example, is attached to the body at the shoulder and, in the course of everyday exploratory and performatory activity, is wielded, hefted, flexed and so on. Accordingly, manipulating a limb's mass distribution ought to influence perception of the limb—quite possibly its felt direction, even perhaps its felt extent.

A historical and frequently voiced view of proprioperception is that it entails a model or schema of the body. Investigations of dynamic touch inspired a very different view: the body schema is the disposition of each limb and limb segment perceived according to the instantaneous states of the inertia ellipsoid field comprising the inertia ellipsoids at each joint [22,50]. The body schema so defined is flexible and 'on line'. (In the ecological perspective, both the environment and the body are their own best models.)

The limbs-as-inertia-ellipsoids view led Pagano & Turvey [50] to the idea that a splint attached to the arm, so weighted as to divert the arm's eigenvector from coincidence with the arm's longitudinal axis, should systematically affect the felt direction of the arm. Pointing at a visible target with a splinted occluded arm supports the expectation (e.g. [51]) as do (i) positioning a single occluded and splinted fore-arm either parallel to the ground or at a 45° angle [51] and (ii) orienting occluded differentially splinted fore-arms relative to each other [52]. The variable of relevance, however, proves to be not the vector of the

second moment (the orientation of the arm's inertia ellipsoid), as originally postulated but, rather, the vector of the first moment—the direction of the arm's centre of mass [53,54].

The results on dynamic touching of limb direction implicate a physical reference frame for limbs, not a spatial (anatomical) reference frame. In this regard, prisms have been used to break the coincidence of the arm's visual and actual positions, and splints have been used to break the coincidence of the arm's physical and anatomical reference frames [55]. The prism and splint effects proved to be additive, pointing to an independence of physical reference frames, possibly achieved by the nesting of haptic proprioperception within visual proprioperception.

9. DYNAMICALLY TOUCHING GROUND DISTANCE FROM HERE TO THERE

Dynamic touching is at work exteroceptively whenever the body is displaced by muscle power (e.g. legged locomotion) relative to the substrate. A mobile organism can come to know about the environment, and its relation to it, by extended episodes of mechanical, tactile contact. In his Essay Toward a New Theory of Vision, Berkeley [56] asserted that a human measures distance by 'the motion of his body, which is perceivable by touch' (p. 188). That legged locomotion without vision is a measure of distance is suggested by investigations with mammals, arachnids, arthropods and insects (see summary in [57]). A simple homing task has been used with blindfolded human participants [58]. On any given trial, a participant went from a fixed starting point A to a variable terminus B-signalled during locomotion by the experimenter-and then attempted to return to A. From A to B (distances from 5 to 50 m), the participants either walked with the aid of a long cane to prevent veering from the path or jogged with the aid of a sighted partner, similarly to prevent veering from the path. From B to A, participants walked alone with the aid of a long cane and without distraction. The return trip matched the outgoing trip and did so equally for both modes of A-B measurement, walking and jogging [58]. Taking the accuracy of the return trip as the index of perceived distance in the outgoing trip, the implication is that distance is perceptible by legged locomotion and is so indifferent to travel duration, number of steps and style of locomotion (participants also measured A-B by combinations of systematic variations in step cadence and step length; [58]).

Apparently, the human odometer (and perhaps legged odometers more generally) is not a pedometer or a stride integrator. Understanding it may require a willingness to think more abstractly about the smart instruments manifest in dynamic touching. The polar planimeter is often used to highlight the level of abstraction [25]. This mechanical organization of a wheel and two rods, one fixed and one mobile, achieves an area measure of any irregular planar form by integrating the line integral of a vector field with constant curl. Are measures of similar abstraction, detectable by dynamic touch, at work in animal odometry?

An important departure point for such considerations is the work of Golubitsky and colleagues [59]. They have argued formally that to encompass the gaits exhibited by bipeds, quadrupeds, hexapods, etc., requires a network (commonly known as a central pattern generator) of twice as many cells (oscillators, systems of ordinary differential equations) as the animal has legs. The periodic solutions of these cells come in two symmetry types: spatial (fixing the solution at each point in time), and spatio-temporal (fixing the solution only after a phase shift). In respect to bipeds, the bipedal network's symmetry consists of the transpositions $\rho = (12) (34)$, $\tau = (13) (24)$, and $\rho \tau = (14) (23)$, where cells 1 and 3 regulate the left leg and cells 2 and 4 regulate the right leg [60]. A primary bipedal gait (walk, run, slow hop, fast hop) is one for which the spatio-temporal symmetries satisfy the dihedral group \mathbf{D}_2 (consisting of rotations and reflections). All three transpositions are entailed. A secondary bipedal gait (skip, gallop-run, gallop-walk, hesitation walk) is one for which the spatio-temporal symmetries approximate the cyclic group \mathbb{Z}_2 (consisting only of rotations). Only one transposition is entailed.

In terms of the primary-secondary distinction, Turvey *et al.* [57] showed that, for the distances tested, if the measure gait (from A to B) and the report gait (from B to A) were of the same symmetry class, then Berkeley's hypothesis held; if the measure and report gaits were from different symmetry classes, then Berkeley's hypothesis did not hold.

The conditions for satisfying Berkeley's hypothesis with respect to a distance d are not, therefore, at the level of the act of legged traversal of d. They are not at the level of locomotion as 'measure' but at the level comprising locomotion as measure and locomotion as 'report'. Efforts to understand the smart odometer implemented by dynamic touching must encompass the measure-report system. A secondary gait as measure and a primary gait as report is a case in which distance is measured by an instrument of symmetry $\approx \mathbf{Z}_2$ and reproduced by an instrument of symmetry \mathbf{D}_2 . The challenge for the human odometer (and the scientist who would study it) is inter-converting distances, one defined by cyclic symmetry and one defined by dihedral symmetry. The experiments reported by Turvey et al. [57] suggest that the D_2 report compresses the $\approx Z_2$ measure. Experiments in progress suggest that the $\approx \mathbb{Z}_2$ report *expands* the \mathbb{D}_2 measure. Dynamic touching holds many surprises.

10. DYNAMICALLY TOUCHING PLACES

Place learning, becoming oriented to places such as home and feeding sites, entails vectors tied to individual landmarks and, depending on the species and the mode of exploratory activity, relations among landmarks. Most inquiry into place learning has focused upon the exploratory activity of looking. Relatively little has considered place learning through the exploratory activity of (dynamic) touching.

In darkness, the tropical wandering spider *Cupien*nius salei deploys the first pair of legs to probe the adjacent surface layout [61]. When the probing forelegs contact a small object (e.g. 10 mm in height), forward locomotion is arrested, the object is explored and the body is elevated so as to cross the object without collision and resume forward locomotion. The walking legs, whether eight or six, are subject to patterns of ground reaction forces, and thereby patterns of strain in the exoskeleton, that are specific to the slope, mechanical resistance (surface viscosity) and, presumably, various other substrate properties of relevance to nocturnal place learning and navigation [60]. Local variations in ground properties detectable by touching have been shown to serve as landmarks for place finding by the whip spider [62] and the desert ant [63].

To investigate place learning strictly by mechanical contact, Harrison & Turvey [64] constructed minimal environments to be explored by blindfolded human participants. Each involved a linear path of 30 m that the participants traversed back and forth, encountering landmarks and a mechanically indistinct location identified by the experimenter as 'home'. The extremes of the path, places where locomotion was reversed, were designated 'north' and 'south'. The landmarks were raised steps. There were three experiments, distinguished by the number of raised steps (one, two or three) defining the minimal environment. The mechanical contacts with each minimal environment were those of walking, stepping and probing with a soft-tipped cane.

The blindfolded participants in each experiment spent minimally an hour in the environment prior to testing, adapting their exploratory and performatory behaviours and engaging in experimenter-conducted activities designed to give them experience in orienting to home from different locations in the environment. In the experimental tests of finding home from a given test location, one landmark or two landmarks for the experimental group were shifted (unbeknown to participants). For the control group, the landmarks remained as they had been during adaptation and training. In the trials comprising these experimental tests, the test location was reached by routes that (i) could have the participant facing or not facing in the direction of home, and (ii) traversing the environment and contacting the landmarks four times or twice.

In a one-landmark environment, perceived home shifted in the same direction, with the same magnitude, as the shifted landmark. In an environment of two landmarks located in the same direction from home (e.g. both to the north), shifting the further landmark towards home resulted in a change in home's perceived location that preserved the original ratio of distances separating home, nearer landmark, and further landmark. Both findings were invariant over the travel route to the test location and repetitions of testing.

The two findings therefore answered a key question in the study of place learning: whether it results in attunement to relations among landmarks as well as attunement to landmark-based vectors [65]. Harrison & Turvey [64] concluded that for humans without the benefits of exploring by looking (and, perhaps, for other organisms that must orient to their surroundings mechanically), the vectors and relations specifying places are revealed and acquired by dynamic touching. As in dynamic touching by wielding, dynamic touching by locomotion reveals what does not change, what is invariant over the exploratory activity.

11. EPILOGUE: HUMANS AS MODELS FOR ANIMALS

Research on dynamic touching, typically conducted with humans, provides insights into the capabilities of non-human organisms. The advantage of the human experimental participant is that a simple instruction, establishing an intention, can render human perception-action as a functional equivalent of a given organism's perception-action. The insights provided are in respect to the potential variables that the organisms could exploit. Two examples are given.

One example is an analogue of exploring an aperture with whiskers or antennae to discern its status as an aperture: Is it 'pass through-able'? Human participants explore an occluded gap by striking its inner edges with a hand-held rod. For a given aperture size S at a distance D in a plane perpendicular to the body's sagittal plane, and a given limb segment plus probe, a collective, dimensionless mechanical parameter λ can be identified that is invariant over the torques, impulses and motions associated with striking the aperture's inner surfaces. Perceived S is a single-valued function of λ (for summaries, see [21,22]). Actual S, however, is not. The property λ of the mechanical energy distribution is not specific to actual S but to the fixed spatial and kinetic properties defining a given situation of probing a separation between surfaces. The perceptible property is not S per se but, perhaps, something more like sizeat-a-distance-contacted-with-a-particular implement ([22], §F).

The other example is an analogue of prey location in a web. The 'information about' carried in the vibrations are often imposed, but they are also obtained by the spider setting the web into vibration. A minimal model system for studying this capability with human 'spiders' is perceiving the distance of a non-visible object on a single taut strand (a minimal haptic web) either vibrated by the spider (the participant) or by the 'intruder' (the experimenter). Vibrations were initiated manually by a sharp, single shake.

The single strand's dynamics are those of the one-dimensional wave equation. In this equation, the elastic force is coupled to the strand's motions by the constant ratio of the strand's linear density μ to the strand's tension T (the horizontal component of force on the strand). For spider-induced vibrations, object distances of 30.5, 61, 91, 122 and 152 cm were perceived, without practice in the task, at (mean values of) 48.3, 66, 83.4, 101.6 and 141.6 cm. Perceived distances were similarly ordered well, but with less accuracy, when vibrations were 'intruder induced'. The significance of T, and thereby μ/T , to this arachnid variant of dynamic touching was demonstrated via manipulations of the hand's position on the strand. (For a summary, see [22].)

The preceding two examples amplify observations made in prior sections and lead to the following concluding remarks. In dynamic touching by humans, there is a logical continuity between (i) perceiving that which is in the hand, or strapped to the foot, or appended to the

torso, and (ii) perceiving by means of that which is attached to hand, or foot, or torso (e.g. [15]). Common principles govern (i) and (ii) in humans and, in our view, are likely to do so for analogues of (i) and (ii) in other species. Thus, we would expect this logical continuity to hold for perceiving keratinous appendages (to the skin or exoskeleton, such as the vibrissae of rodents and the antennae of crayfish and insects) and perceiving by means of keratinous appendages [66]. The significance of the logical continuity when generalized is conveyed by Burton ([66], p. 117): 'The prevalence of keratinous appendages for animals in different phyla represents the recruitment for receptor function of body parts that do not fit the classic receptor profiles, being neither nervous nor living. This recruitment shows that what qualifies a potential receptor is not necessarily nervous supply but simply a susceptibility to physical influence, and keratinous material can be influenced just as predictably as living tissue'.

In this epilogue, we have recognized the human animal as a model system—a potential source of experimental data and theory valuable to understanding active touch in non-human animals. The review we have given of dynamical (effortful) touching in the preceding sections has articulated the 'susceptibility to physical influence' to which Burton refers. Further inquiry into this susceptibility within the human model, coordinate with studies of rodents, crayfish and insects, should advance appreciation of the perceiving achieved by 'whisking' vibrissae and 'waving' antennae.

This research was supported by the National Science Foundation.

REFERENCES

- 1 Reed, E. S. 1996 *Encountering the world: toward an ecological psychology.* Oxford, UK: Oxford University Press.
- 2 Gibson, J. J. 1966 The senses considered as perceptual systems. Boston, MA: Houghton Mifflin.
- 3 Gibson, J. J. 1979 *The ecological approach to visual perception.* Boston, MA: Houghton Mifflin.
- 4 Turvey, M. T. & Shaw, R. E. 1995 Toward an ecological physics and a physical psychology. In *The science of the mind: 2001 and beyond* (eds R. Solso & D. Massaro), pp. 144-169. Oxford, UK: Oxford University Press.
- 5 Margulis, L. & Schwartz, K. V. 1982/1998 *Five kingdoms*. San Francisco, CA: W. H. Freeman.
- 6 Lee, D. N. 1978 The functions of vision. In *Modes of perceiving and processing information* (eds H. L. Pick Jr, & E. Saltzman Jr,), pp. 159–170. Hillsdale, NJ: Erlbaum.
- 7 Hanke, W. & Bleckmann, H. 2004 The hydrodynamic trails of *Lepomis gibbosus* (Centrarchidae), *Colomesus psittacus* (Tetraodontidae) and *Thysochromis ansorgii* (Cichlidae) measured with scanning particle image velocimetry. *J. Exp. Biol.* 207, 1585–1596. (doi:10.1242/jeb.00922)
- 8 Miersch, L., Hanke, W., Wieskotten, S., Hanke, F. D., Oeffner, J., Leder, A., Brede, M., Witte, M. & Dehnhardt, G. 2011 Flow sensing by pinniped whiskers. *Phil. Trans. R. Soc. B* 366, 3077–3084. (doi:10.1098/ rstb.2011.0155)
- 9 Turvey, M. T. & Fonseca, S. 2009 Nature of motor control: perspectives and issues. In *Progress in motor control: a multidisciplinary perspective* (ed. D. Sternad), pp. 93–123. New York, NY: Springer Verlag.
- 10 Rieffel, J., Trimmer, B. & Lipson, H. 2008 Mechanism as mind: what tensegrities and caterpillars can teach us

about soft robotics. In Artificial Life XI: Proc. 11th Conf. on the Simulation and Synthesis of Living Systems (eds S. Bullock, J. Noble, R. Watson & M. A. Bedau), pp. 506-512. Cambridge, MA: MIT Press.

- 11 Ingber, D. E. 2008 Tensegrity-based mechanosensing from macro to micro. *Prog. Biophys. Mol. Biol.* 97, 163–179. (doi:10.1016/j.pbiomolbio.2008.02.005)
- 12 Motro, R. 2003 *Tensegrity: structural systems for the future.* Sterling, VA: Kogan Page Science.
- 13 Skelton, R. E. & de Oliviera, M. C. 2009 Tensegrity systems. New York, NY: Springer.
- 14 Silva, P. L., Fonseca, S. & Turvey, M. T. 2010 Is tensegrity the functional architecture of the equilibrium point hypothesis? *Motor Control.* **14**, e35–e40.
- 15 Carello, C., Fitzpatrick, P. & Turvey, M. T. 1992 Haptic probing: perceiving the length of a probe and the distance of a surface probed. *Percept. Psychophys.* 51, 580-598. (doi:10.3758/BF03211655)
- 16 Solomon, H. Y. & Turvey, M. T. 1988 Haptically perceiving the distances reachable with hand-held objects. J. Exp. Psychol. Hum. Percept. Perform. 14, 404-427. (doi:10.1037/0096-1523.14.3.404)
- 17 Bingham, G. P. 1993 Perceiving the size of trees: forms as information about scale. J. Exp. Psychol. Hum. Percept. Perform. 19, 1139–1161. (doi:10.1037/0096-1523.19.6.1139)
- 18 Solomon, Y. 1988 Movement produced invariants in haptic explorations: an example of a self-organizing, information-driven, intentional system. *Hum. Movement Sci.* 7, 201–223. (doi:10.1016/0167-9457(88)90012-7)
- 19 Fitzpatrick, P., Carello, C. & Turvey, M. T. 1994 Eigenvalues of the inertia tensor and exteroception by the 'muscular sense'. *Neuroscience* **60**, 551–568. (doi:10.1016/0306-4522(94)90264-X)
- 20 Turvey, M. T., Burton, G., Amazeen, E. L., Butwill, M. & Carello, C. 1998 Perceiving the width and height of a hand-held object by dynamic touch. *J. Exp. Psychol. Hum. Percept. Perform.* 24, 35–48. (doi:10.1037/0096-1523.24.1.35)
- 21 Carello, C. & Turvey, M. T. 2000 Rotational invariants and dynamic touch. In *Touch, representation and blindness* (ed. M. Heller), pp. 27–66. Oxford, UK: Oxford University Press.
- 22 Turvey, M. T. & Carello, C. 1995 Dynamic touch. In Handbook of perception and cognition. Perception of space and motion, vol. 5 (eds W. Epstein & S. Rogers), pp. 401–490. New York, NY: Academic Press.
- 23 Ashby, F. G. & Townsend, J. T. 1986 Varieties of perceptual independence. *Psychol. Rev.* 93, 154–179. (doi:10. 1037/0033-295X.93.2.154)
- 24 Maddox, W. T. & Ashby, F. G. 1996 Perceptual separability, decisional separability, and the identificationspeeded classification relationship. *J. Exp. Psychol. Hum. Percept. Perform.* 22, 795–817. (doi:10.1037/ 0096-1523.22.4.795)
- 25 Runeson, S. 1977 On the possibility of smart perceptual mechanisms. *Scand. J. Psychol.* 18, 172–179. (doi:10. 1111/j.1467-9450.1977.tb00274.x)
- 26 Solomon, H. Y., Turvey, M. T. & Burton, G. 1989 Perceiving rod extents by wielding: haptic diagonalization and decomposition of the inertia tensor. *J. Exp. Psychol. Hum. Percept. Perform.* 15, 58–68. (doi:10.1037/0096-1523.15.1.58)
- 27 Hajnal, A., Fonseca, S. T., Harrison, S., Kinsella-Shaw, J. M. & Carello, C. 2007 Comparison of dynamic (effortful) touch by hand and foot. *J. Motor Behav.* **39**, 82–88. (doi:10.3200/JMBR.39.2.82-88)
- 28 Palatinus, Z., Carello, C. & Turvey, M. T. 2011 Principles of selective perception by dynamic touch extend to the torso. *J. Motor Behav.* 43, 87–93. (doi:10.1080/00222895.2010.538767)

- 29 Carello, C., Santana, M. V. & Burton, G. 1996 Selective perception by dynamic touch. *Percept. Psychophys.* 58, 1177–1190. (doi:10.3758/BF03207551)
- 30 Michaels, C. F. & Isenhower, R. W. 2011 Information space is action space: perceiving the partial lengths of rods rotated on an axle. *Atten. Percept. Psychophys.* 73, 160-171. (doi:10.3758/s13414-010-0024-3)
- 31 Turvey, M. T., Park, H.-S., Dumais, S. P. & Carello, C. 1998 Nonvisible perception of segments of a handheld object and the attitude spinor. *J. Motor Behav.* 30, 3–19. (doi:10.1080/00222899809601318)
- 32 Turvey, M. T., Carello, C., Fitzpatrick, P., Pagano, C. C. & Kadar, E. E. 1996 Spinors and selective dynamic touch. *J. Exp. Psychol. Hum. Percept. Perform.* 22, 1113–1126. (doi:10.1037/0096-1523.22.5.1113)
- 33 Hestenes, D. 1994 Invariant body kinematics: I. Saccadic and compensatory eye movements. *Neural Netw.* 7, 79–88. (doi:10.1016/0893-6080(94)90057-4)
- 34 Hestenes, D. 1994 Invariant body kinematics: II. Reaching and neurogeometry. *Neural Netw.* 7, 65–77. (doi:10. 1016/0893-6080(94)90056-6)
- 35 Turvey, M. T. 1996 Dynamic touch. Am. Psychol. 51, 1134–1152. (doi:10.1037/0003-066X.51.11.1134)
- 36 Cabe, P. A. 2010 Sufficiency of longitudinal moment of inertia for haptic cylinder length judgments. J. Exp. Psychol. Hum. Percept. Perform. 32, 300-313.
- 37 Kingma, I., van de Langenberg, R. & Beek, P. J. 2004 Which mechanical invariants are associated with the perception of length and heaviness of a nonvisible handheld rod? Testing the inertia tensor hypothesis. *J. Exp. Psychol. Hum. Percept. Perform.* **30**, 346–354. (doi:10.1037/0096-1523.30.2.346)
- 38 Burton, G. & Turvey, M. T. 1990 Perceiving the lengths of rods that are held but not wielded. *Ecol. Psychol.* 2, 295–324. (doi:10.1207/s15326969eco0204_1)
- 39 Stroop, M., Turvey, M. T., Fitzpatrick, P. & Carello, C. 2000 Inertia tensor and weight-percept models of length perception by static holding. *J. Exp. Psychol. Hum. Percept. Perform.* 26, 1133–1147. (doi:10.1037/ 0096-1523.26.3.1133)
- 40 Carello, C., Fitzpatrick, P., Domaniewicz, I., Chan, T.-C. & Turvey, M. T. 1992 Effortful touch with minimal movement. *J. Exp. Psychol. Hum. Percept. Perform.* 18, 290–302. (doi:10.1037/0096-1523.18.1.290)
- 41 Riley, M. A., Wagman, J. B., Santana, M.-V., Carello, C. & Turvey, M. T. 2002 Perceptual behavior: recurrence analysis of a haptic exploratory procedure. *Perception* **31**, 481–510. (doi:10.1068/p3176)
- 42 Webber Jr, C. L. & Zbilut, J. P. 1996 Assessing deterministic structures in physiological systems using recurrence plot strategies. In *Bioengineering approaches* to pulmonary physiology and medicine (ed. M. C. K. Khoo), pp. 137–148. New York, NY: Plenum.
- 43 Lederman, S. J. & Klatzky, R. L. 1987 Hand movements: a window into haptic object recognition. *Cogn. Psychol.* 19, 342–368. (doi:10.1016/0010-0285(87)90008-9)
- 44 Peng, C.-K., Havlin, S., Stanley, H. E. & Goldberger, A. L. 1995 Quantification of scaling exponents and crossover phenomena in nonstationary heartbeat time series. *Chaos* 5, 82. (doi:10.1063/1.166141)
- 45 Singer, J. D. & Willett, J. B. 2003 Applied longitudinal data analysis: modeling change and event occurrence. New York, NY: Oxford University Press.
- 46 Stephen, D. G., Arzamarski, R. & Michaels, C. F. 2010 The role of fractality in perceptual learning: exploration in dynamic touch. *J. Exp. Psychol. Hum. Percept. Perform.* 36, 1161–1173. (doi:10.1037/a0019219)
- 47 Carello, C. & Wagman, J. B. 2009 Mutuality in the perception of affordances and the control of movement. In

Progress in motor control (ed. D. Sternad), pp. 273–292. New York, NY: Springer Verlag.

- 48 Amazeen, E. L. & Turvey, M. T. 1996 Weight perception and the haptic size-weight illusion are functions of the inertia tensor. J. Exp. Psychol. Hum. Percept. Perform. 22, 213-232. (doi:10.1037/0096-1523.22.1.213)
- 49 Shockley, K., Carello, C. & Turvey, M. T. 2004 Metamers in the haptic perception of heaviness and moveableness. *Percept. Psychophys.* 66, 731–742. (doi:10.3758/ BF03194968)
- 50 Pagano, C. & Turvey, M. T. 1995 The inertia tensor as a basis for the perception of limb orientation. *J. Exp. Psychol. Hum. Percept. Perform.* 21, 1070–1087. (doi:10. 1037/0096-1523.21.5.1070)
- 51 Garrett, S., Pagano, C., Austin, G. & Turvey, M. T. 1998 Spatial and physical frames of reference in positioning a limb. *Percept. Psychophys.* **60**, 1206–1215. (doi:10.3758/ BF03206170)
- 52 Pagano, C., Garrett, S. & Turvey, M. T. 1996 Is limb proprioception a function of the limbs' inertial eigenvectors? *Ecol. Psychol.* 8, 43–69. (doi:10.1207/s15326 969eco0801_3)
- 53 van de Langenberg, R., Kingma, I. & Beek, P. J. 2008 The perception of limb orientation depends on the center of mass. *J. Exp. Psychol. Hum. Percept. Perform.* 34, 624–639. (doi:10.1037/0096-1523.34.3.624)
- 54 Silva, P. L. 2009 Role of haptic information in shaping coordination dynamics. PhD thesis, University of Connecticut, CT.
- 55 Riley, M. A. & Turvey, M. T. 2001 The self-organizing dynamics of intentions and actions. Am. J. Psychol. 114, 160–169. (doi:10.2307/1423388)
- 56 Berkeley, G. 1948 Essay toward a new theory of vision. In The works of George Berkeley, Bishop of Cloyne, vol. 1 (eds A. A. Luce & T. E. Jessop), pp. 159–239. London, NY: Nelson & Sons. (Original work published 1709).
- 57 Turvey, M. T., Romaniak-Gross, C., Isenhower, R. W., Arzamarski, R., Harrison, S. & Carello, C. 2009 Human odometer is gait-symmetry specific. *Proc. R. Soc. B* 276, 4309–4314. (doi:10.1098/rspb.2009.1134)
- 58 Schwartz, M. 1999 Haptic perception of the distance walked when blindfolded. J. Exp. Psychol. Hum. Percept. Perform. 25, 852–865. (doi:10.1037/0096-1523.25.3.852)
- 59 Golubitsky, M., Stewart, I., Buono, P.-L. & Collins, J. J. 1999 Symmetry in locomotor central pattern generators and animal gaits. *Nature* 401, 693–695. (doi:10.1038/ 44416)
- 60 Pinto, C. A. & Golubitsky, M. 2006 Central pattern generators for bipedal locomotion. *J. Math. Biol.* 53, 474–489. (doi:10.1007/s00285-006-0021-2)
- 61 Barth, F. G. 2002 A spider's world sense and behavior. New York, NY: Springer-Verlag.
- 62 Santer, R. D. & Hebets, E. A. 2009 Tactile learning by a whip spider, *Phrynus marginemaculatus* C. L. Koch (Arachnida, Amblypygi). *J. Comp. Physiol. A* 195, 393–399. (doi:10.1007/s00359-009-0417-8)
- 63 Seidl, T. & &Wehner, R. 2006 Visual and tactile learning of ground structures in desert ants. J. Exp. Biol. 299, 3336-3344. (doi:10.1242/jeb.02364)
- 64 Harrison, S. & Turvey, M. T. 2010 Place learning by mechanical contact. *J. Exp. Biol.* 213, 1436–1442. (doi:10.1242/jeb.039404)
- 65 Collett, T. S. & Zeil, J. 1998 Places and landmarks: an arthropod perspective. In *Spatial representation in animals* (ed. S. Healy), pp. 18–53. Oxford, UK: Oxford University Press.
- 66 Burton, G. 1993 Non-neural extensions of haptic sensitivity. *Ecol. Psychol.* 5, 105–124. (doi:10.1207/ s15326969eco0502_1)