Haptic Illusions induced by Tactile Flow

Antonio Bicchi, Davide Dente, Enzo Pasquale Scilingo

Interdepartmental Research Centre "E. Piaggio", University of Pisa,
via Diotisalvi, 2 56126 Pisa, Italy
Tel. +39-0505553639 Fax: +39-050550650
E-mail: bicchi@ing.unipi.it; dente@piaggio.ccii.unipi.it; e.scilingo@ing.unipi.it

Abstract. In this paper we report on a set of experiments involving perceptual illusions elicited by dynamic tactile stimulation of fingertips. These misperceptions are akin to some well studied optical illusions, which have been given an explanation in terms of the mechanisms of optic flow perception. We hypothesize that a similar perceptual mechanism exists for tactile flow, which is related to how humans perceive relative motion and pressure between the fingertips and objects in contact. We present a computational model of tactile flow, and discuss how it relates to accepted models of the neurophyisiology of touch. A particularly interesting phenomenon observed under some experimental circumstances, consisting of an incoherent tactile perception generating what we call a *tactile vertigo*, can be explained in terms of this model. The proposed tactile flow model also explains other phenomena observed in the past (namely, the Contact Area Spread Rate effect), and is of importance in designing simpler, more effective devices for artificial haptic sensing and displays.

1 INTRODUCTION

The state of the art of haptic display technologies has witnessed a dramatic progress over the last decade or so, and can be considered as rather satisfactory as far as display devices in the kinesthetic domain are considered. Indeed, most commercial and experimental devices can only render macroscopic force-position relationships, and involve a limited portion of an operator's haptic sensory apparatus.

There is a wide consensus that, to move towards more convincing haptic displays, the cutaneous channel of haptic perception should be better addressed. Opposing to this are however, on one side, the complexity of implementing a sufficiently detailed and accurate mechanical stimulation of the skin. On the other hand, the need is widely felt for a deeper understanding of the sense of touch in humans, which may enable better technological solutions. An example of the expected benefits is through the study of the very limitations of our senses, which may be exploited to "cheat" the operator in believing a different sensation from what the mere stimulus is.

The study of illusions has been traditionally a rich source of insight in the neurophysiology and psychophysics of perception, especially in vision. In this paper, we study the haptic correlates of a particular class of visual illusions, those related to optic flow. We report on four psychophysical experiments related to how humans perceive relative motion and pressure between the fingertip and objects in contact. These experiments highlight the existence of similarities between the mechanisms of perception of dynamic stimuli in the two sensorial modalities. We hence propose the term *tactile flow* for describing these effects, and present a computational model of flow that generalizes upon current descriptions of optic flow, while also providing a satisfactory explanation of experimental observations in tactile flow. We also discuss how the model relates with accepted models of the neurophyisiology of touch.

2 Psychophysical Experiments

We report on a series of three experiments, the first two of which have been conducted originally for this study, while the fourth is reconsidered here in a different perspective than in its original description ([1]).

2.1 Experiment 1

The first experiment is inspired to the so-called *barber pole illusion* in vision, by which an upward motion of diagonal strips is falsely induced from the actual rotational motion of the pole (see e.g. [7]). The experimental apparatus (depicted in fig. 1) consisted in a linear motorized slide with changing orientation, onto which a textured pad can be fixed at different angles. The pad is realized in

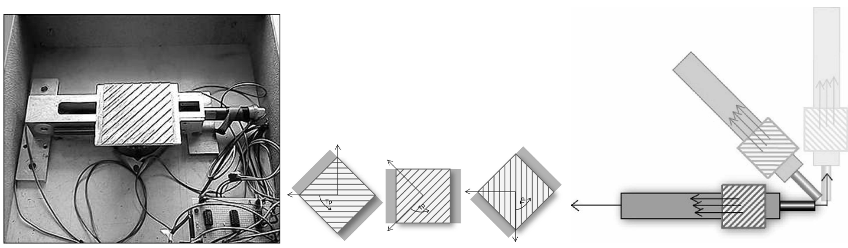

Fig. 1. Experimental apparatus for experiment 1: physical appearance (left); changing the pad texture orientation (middle); changing the slide orientation (right).

aluminum, and presents a series of 1-mm high, 1-mm wide ridges separated by 1-cm wide grooves. An opening of about the size of a human forefinger was made on the cover, so as to allow contact of the subject's finger with the pad. The experiment consisted in keeping the finger still, while the pad was moved slowly by the slide in a direction unknown to the subject, while being fixed on the slide at an angle also unknown (2). A small curtain was used to prevent subjects from seeing the pad motion. In different subsequent tests, the direction of motion of the slide was set to 0 degrees (motion perpendicular to the subject's finger), 45, and 90 degrees (motion aligned with the finger). For each orientation of the slide, the pad texture could be placed at different angles, ranging from 0 to 150

Fig. 2. Volunteer during an experimental test.

degrees, relative to the fingertip. In this experiment, a liquid soap was used as a lubricant between the finger and the pad, so as to limit skin stretching due to friction between the finger and the pad. Each subject was asked to determine if any motion was perceived and, if so, to describe the motion direction. Different directions were reported on the cover, and labelled with numbers from 1 to 24, visible to subjects. Answers such as “between direction 3 and 4” were interpreted as 3.5 (resulting in a resolution of 7.5 degrees). 47 subjects (Fig.2) volunteered to participate to the experiment. Each subject was presented with 24 different combinations of three slide directions (at 0, 45, and 90 degrees) and 8 texture orientations (at 0, 30, 45, 60, 90, 120, 135, and 150 degrees) in random order, for a grand total of 1128 trials. Before making a decision, a subject could ask for repetitions of the task.

Experimental results are reported in fig. 3, plotting the angle between the perceived and actual direction of motion (on the vertical axis) versus the angle between the direction of motion of the pad and the orientation of texture (horizonal axis). It can be observed that the discrepancy between the actual and perceived direction of motion increases almost linearly with the texture slant. A dashed line is also reported for reference, corresponding to the theoretical case that the perceived direction is always perpendicular to the texture, independently of the actual direction of motion. Such ideal case, corresponding to a perfectly illusory motion, is what is typically obtained with the optical barber pole illusion.

In experiments where the texture was aligned with the slide motion, no illusion is to be expected, consistently with the optical illusion counterpart. Indeed, in this case, 65% of the subjects reported that there was no motion at all (which is again the expected answer in the analogous visual experiment), while (35)% reported an approximately correct direction of motion (no illusory response). For consistency’s sake, these data have not be reported in the graph of fig.3.

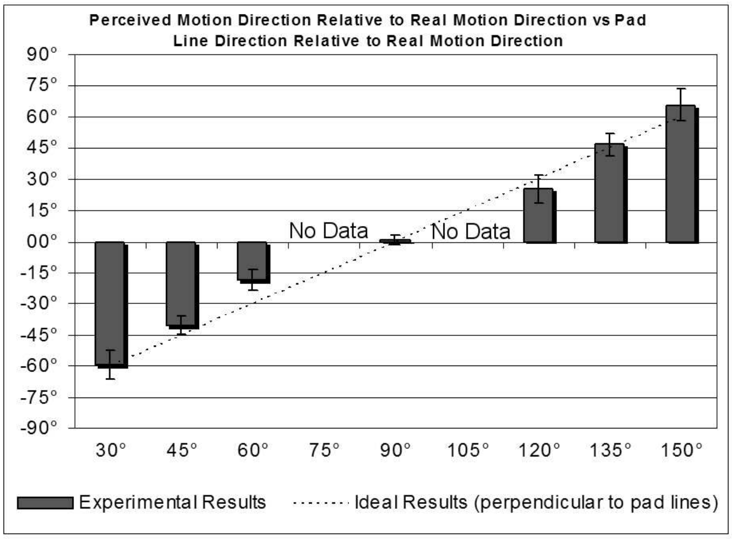

Fig. 3. Results of the tactile *barber pole* experiment. The dashed line indicates a perfectly illusory response.

2.2 Second experiment

The second experiment was aimed at studying the effects of friction on tactile perception of relative motion. The experimental apparatus and methods were similar to the previous experiment, but in this case no lubrication was used. Furthermore, three different pads were used, consisting of a single ridge (see fig. 4). The pads differed only by the ridge width, that was 0.5 mm, 10 mm, and 20 mm, respectively, while the ridge's height was 1mm in all three pads. The

Fig. 4. Three pads used in the second experiment.

increasing width of the ridges produces an increasing friction effect while the pad is moved (according to the procedures described above) with respect to the fingertip. Thirty subjects took part in this experimental session. Every subject touched the three different moving pads in sequence. Ridge inclination for all the tests was of 45 degrees, while the slide has always been oriented to 0 degrees.

Results of this experiment are reported in fig. 5, comparing again the data on the perceived direction of motion, with the ideal illusory direction (dashed line) perpendicular to the ridge. These results show that the illusory perception of motion is greatly reduced by higher levels of friction, and almost disappears in the wide ridge case.

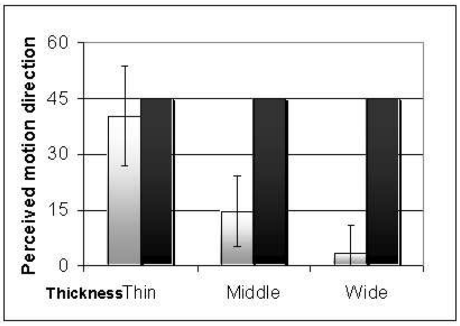

Fig. 5. Results of the second experiment, with substantial friction between the fingertip and the moving pattern.

In performing this experiment, it was observed that subjects frequently requested to repeat the test many times with each pad, and reported of their "being confused" about the perceived motion. In several cases, especially in tests with the two thinner ridges, 19% of subjects reported perceiving either a rotating motion or two simultaneous motions (these results are expunged from those in fig. 5). We will refer to such apparent confusion induced in subjects by these experiments as to a *tactile vertigo*.

2.3 Experiment 3

In this experiment we investigate active tactile exploration. The optical illusion to which this experiment is inspired, depicted in fig.6-left), consists in perceiving the edges of a square, drafted within a pattern of concentric circles, as if curved towards the center. A pad with a series of concentric circular ridges (1mm high and wide, spaced by 2.2mm in the radial direction) and a rectilinear ridge (2mm high and wide, and 55mm long), was realized in aluminum (see fig.6-right). A similar tactile pad, without concentric circles, was used for reference. The surface of both pads was lubricated with a liquid soap. Thirty blinded subjects were asked to haptically explore the pad at their will, and to finally report about the shape of the higher ridge. If a subject reported it to be be curved, the direction of its concavity was further asked. Each subject performed five explorations, three of which on the test pad and two on the reference pad, presented in random order. Experimental results indicated that 59% of subjects were induced to believe that the ridge was curved, and among these only 2% of subjects reported on an outward concavity. 41% correctly reported the ridge to be straight. All subjects correctly described the shape of the straight ridge on the reference pad.

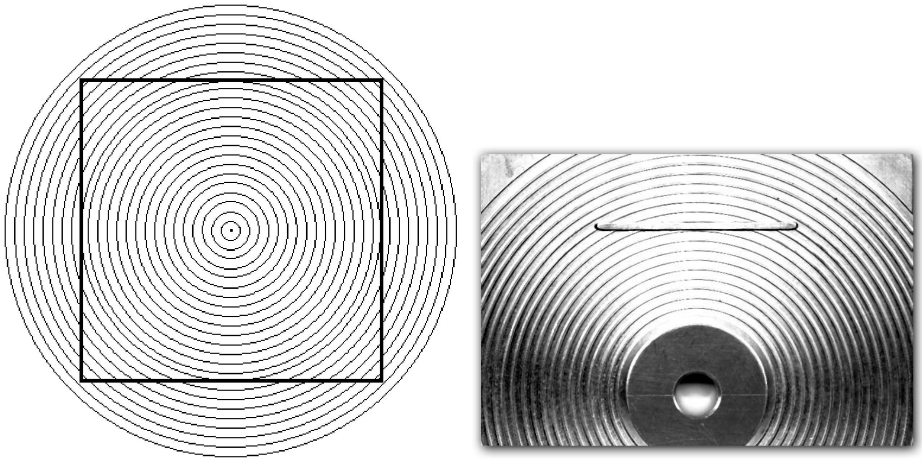

Fig. 6. The optical illusion inspiring the third experiment (left), and the tactile pad used in the experiment.

2.4 Fourth Experiment

The literature on haptic discrimination of softness (e.g. [22],[13]) has clarified that human capabilities in this task depend strongly on cutaneuous information, being proprioceptive perception relatively awkward at this. However, it has later been argued that a significant part of the haptic information used to discriminate softness does not actually rely on detailed sensing of the stress-strain distribution in the skin at and near the contact, rather it is strongly related to how fast the contact area grows when the probing force is increased. This relationship, which bears some resemblance to the information on the velocity of an approaching object (or *time-to-contact* [2]) conveyed by the increase in size of its retinal image, was formalized in the concept of Contact Area Spread Rate (CASR), and validated by means of several psychophysical experiments in [1]. In one of those experiments, 15 volunteers were asked to recognize 5 different items by touch only. Their performance in the recognition task was compared when they were touching the original specimens, or two artificial replicae. These were a device designed to only display a proprioceptive behaviour matched to that of the original, and a device which also allowed to match the original's CASR. Results of these experiments, described in detail in [1], are reported in fig 7 for reference, and show how CASR is indeed extremely useful in our perception of softness by touch.

3 Computational Model of Flow

The experimental results reported above agree well in general with analogous effects observed in visual perception. In that field, studies on this general topic, often referred to as *optic flow*, began rather early [8], and have played quite an important role in the subsequent developments of the science of vision in humans and in the technology of computer vision.

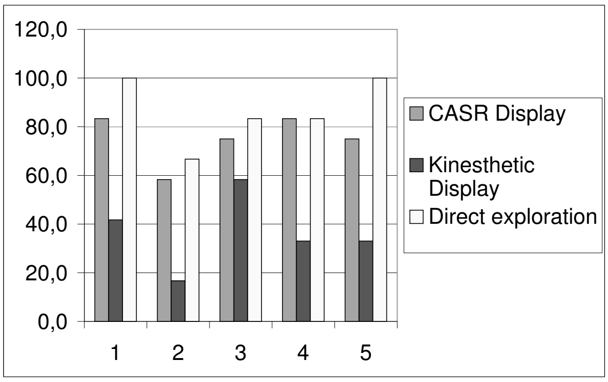

Fig. 7. Percentage of successful recognition of 5 specimens of different softness by direct exploration, and by exploration of two artificial replicae of their proprioceptive and CASR behaviours, respectively.

Properly speaking, optic flow is the distribution of apparent velocities of movement of patterns in an image, arising from relative motion between an object and a viewer. The human brain analyses this flow field to obtain several information about environment. The optic flow field contains proprioceptive, segmentation and exteroceptive information. Proprioceptive information refer to both rotational and translational ego-motion and orientation. Segmentation regards splitting and merging scene zones on the basis of flow discontinuities. Exteroceptive information concerns object position, motion, form and orientation. This information is processed by different cerebral areas: middle temporal (MT) area neurons are selective to direction of translation while middle superior temporal (MST) area neurons are selective to more complex motion patterns, such as radial, circular and spiral motions. Cells in the dorsolateral region of MST (MSTd) have been found to respond selectively to expansion, contractions, rotations, spirals and to multi-component motions [5, 6, 9, 17, 20, 23, 24]. Recent studies have demonstrated that other areas in the parietal lobe, such as the ventral intraparietal cortex (VIP) and area 7a, are highly sensitive to optic flow stimuli [21].

Computational models of optic flow have offered an important stimulus to the development of artificial intelligence, and computer vision in particular, which in many cases resulted in turn in crucial benefits to natural sciences. In particular, computational models of optic flow have attracted wide attention as they can allow predicting expected outcomes of experiments and afford a deeper understanding of investigated phenomena.

A widely accepted model of optic flow, proposed by Horn and Schunck [11], consists in mathematically describing motion in an image sequence via a partial differential equation. This equation involves the spatial coordinates of the image plane (denoted e.g. by x, y), time (t), and the intensity of a physiologically relevant quantity in the image. This is typically brightness in optic flow, which

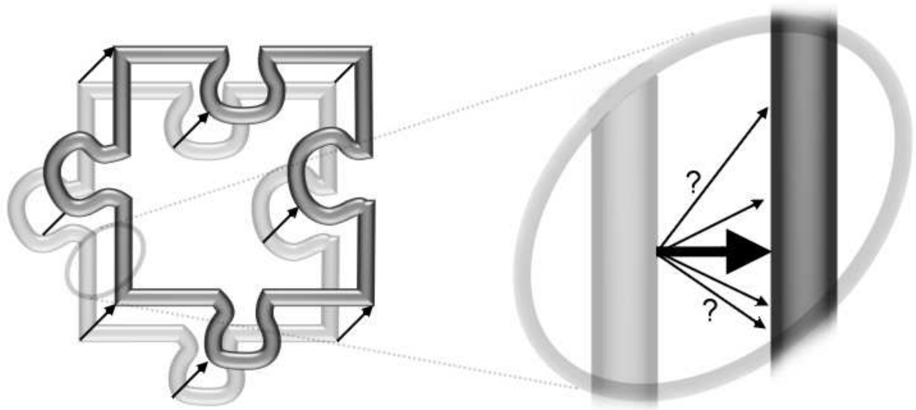

Fig. 8. An illustration of the concept of flow in the two-dimensional case. An iso-intensity curve of a certain level moves to a different position, defining a velocity field. However, having all points on the same curve the same intensity, it is not possible to distinguish their pairwise correspondence. This leaves the tangential component of velocities undefined, and gives raise to the so-called *aperture problem*, which in turn may generate perceptual illusions. The problem is irrelevant for punctual features (e.g., corners), for which the flow is uniquely defined. Punctual features are indeed used by our perceptual system to disambiguate illusory cues.

we will denote as $B(x, y, t)$ here, to show its dependency on independent space and time variables.

The basic idea of the model is that adjacent sets of pixels of equal intensity (iso-intensity curves), associated e.g. with objects contours, move in space through time defining a vectorial flow, that is, associating to each image point at any given instant a direction and velocity of motion. Let $v(x, y, t)$ denote the optic flow, i.e. the 2-dimensional velocity vectors of iso-intensity curves. The optic flow equation is written (assuming that illumination changes are negligible) as

$$\frac{dB}{dt} = \frac{\partial B}{\partial x} v_x + \frac{\partial B}{\partial y} v_y + \frac{\partial B}{\partial t} = 0, \quad (1)$$

or, in vector notation,

$$\frac{\partial B}{\partial (x, y)} v = -\frac{\partial B}{\partial t}. \quad (2)$$

This equation defines the optic flow vector at all image points, except for components that are tangent to the iso-intensity curve itself (i.e., components perpendicular to the spatial brightness gradient $\frac{\partial B}{\partial (x,y)}$). A graphical illustration of the computational definition of flow of iso-intensity curves is given in fig.8. Such incomplete definition of the flow is often referred to as the *aperture problem*, and is crucial in generating a few optical illusions. For instance, the barber pole illusion can be explained by the fact that, being the motion of a linear pattern observed through a window which prevents any distinctive feature to be perceived, then no clue is available indicating whether or not motion occurred along the pattern direction.

In an attempt at generalizing the flow model to tactile perception, there are at least two main issues to be considered. A first important consideration is that the distribution of receptors in the skin is three-dimensional, rather that bidimensional (as the retina is). It is to be expected hence that tactile flow should be concerned with motion of iso-intensity surfaces, rather than curves, and described by a partial differential constraint equation of the type

$$\frac{dI}{dt} = \frac{\partial I}{\partial x}v_x + \frac{\partial I}{\partial y}v_y + \frac{\partial I}{\partial z}v_z + \frac{\partial I}{\partial t} = 0. \tag{3}$$

A second crucial problem is to identify which quantity should be considered as the stimulus intensity here. Indeed, the states of stress and strain within the epidermis and dermis, which influence mechanical receptors in the skin, are both rather complicated distributions of tensorial quantities. On the other hand, the flow model(3) implies a scalar notion of "intensity". Next section provides a neurophysiologically motivated approach at these two questions.

4 Tactile flow and the neurophysiology of touch

To address the above mentioned modeling issues, it is most useful to review the current state of knowledge concerning the neurophysiology of cutaneous mechanoreceptors in the human glabrous skin. We mainly follow [12] in this section.

Merkel corpuscles (SA1 afferents) innervate the skin densely (about 100 per cm^2 at the fingertip), and respond best in a frequency range of 0.3-3Hz. They have two remarkable response properties: their sensitivity to points, edges and curvature, which is a consequence of their selective sensitivity to strain energy density; and their spatial resolution of 0.5mm, overriding their receptive field diameter of just 2-3mm. Because of these two properties, SA1 afferents are responsible for shape, orientation and texture perception. SA1 afferents are at least ten times more sensitive to dynamic than to static stimuli.

Meissner corpuscles (RA afferents) innervate the skin even more densely than the SA1 afferents do (about 150 per cm^2 at the fingertip in man and monkey). They respond best with a frequency range of $3 - 40Hz$ an are four time more sensitive to dynamic skin deformation than are SA1 afferents. RA afferents respond to stimuli over their entire receptive field ($3 - 5mm$) relatively uniformly, hence resolve spatial details poorly. RA afferents transmit a robust neural image of skin motion. RA response begins to saturate at about $100\mu m$ and is insensitive to the height of surface features above $300 - 400\mu m$ [25]. The RA's most important function seems to be the provision of feedback signals for grip control [14].

Ruffini corpuscles (SA2 afferents) are relatively large spindle-shaped structures tied into the local collagen matrix. Because of their position, the SA2 population transmit a neural image of skin stretch, with relatively little interference from objects held in the hand. SA2 afferents innervate the skin less densely than either SA1 or RA afferents, and they have a receptive field five times larger. Thus, SA2 afferents have poor spatial resolution. The SA2's most important function seems to be the provision of hand shape and finger position through the pattern of skin stretch produced by each hand and finger conformation [12][3]. Secondarily, they transmit a neural image of motion direction, when the motion produce skin stretch [16].

Pacini (PC) corpuscles are very rapidly adapting receptors distributed in the deeper part of the dermis, with a very low density and large receptive field. They appear to be mostly involved in high-frequency vibration detection, and crucial in indirect mechanical sensing (such as e.g. in manipulations with a probe or tool). They are less relevant to cutaneous sensing of slowly moving objects or changing pressures.

According to this discussion, it is to be expected that, if tactile flow is to play an actual role in haptic perception, then are the Merkel and Meissner afferents that should be mainly involved. Indeed, as sensitivity to shape and texture is strongly related to dynamic exploration, and SA1 and RA corpuscles are the primary source of shape information, the role of SA1 and RA in mediating dynamic (flow) information (in their respective range of frequency) to shape perception appears very likely. Pacinian corpuscles are probably irrelevant to the phenomenon, due to their very poor resolution, while SA2 may play a more complicated role, that will be considered again later on.

Some evidence can also be found by a psychophysical viewpoint. For instance, [10] shows that tactile information for stimuli increasing at a fixed rate, is more reliably conveyed when the stimulus is skin indentation rather than force intensity. In a similar spirit, experiments have been performed on slowly adapting (SA1) mechanoreceptors in the racoon[19]. When identical mechanical stimuli were repeatedly applied to the receptive field of a SA1 fiber, the responses were more consistent for controlled indentation than for controlled force.

Consistently with the discussion above, we propose that the Strain Energy Density (SDE) is considered as the intensity characterizing tactile flow in (3). Furthermore, the fact that both Merkel and Meissner corpuscles are located very near to the skin surface might suggest that a two-dimensional model of flow, limited to the outer surface of fingertips, could result in an acceptable approximation of the complete three-dimensional model (3).

5 Discussion

In view of the computational model illustrated above, we can attempt an explanation of tactile illusions described earlier in the paper.

The aperture problem of tactile flow explains the first and the third experiment. Indeed, the graphical illustration of fig. 8 holds here as well, if the pattern is thought as the iso-SDE curve induced by contact on the superficial layer of the skin by the indenter.

The second experiment may entail a more complicated explanation. Indeed, we have here that the higher friction involved at the contact causes adhesion between the moving pad and the skin surface, hence the skin is stretched in the direction of motion of the slide. Such stretch stimulates Ruffini corpuscles' response, eliciting an information revealing the actual motion direction. This information is inconsistent with the information integrated from SA1 and RA responses by an aperture-prone perceptual mechanism. Hence the difficulty of subjects to reconcile such inconsistent cues, and the phenomenon above referred to as *tactile vertigo*.

Finally, also the fourth experiment can be directly related to tactile flow, and in particular to its integral version ([2]). Indeed, the contact area corresponds to the measure of the surface contained within an iso-SDE curve on the finger surface, which grows with the contact force at a different rate depending on the material properties. This effect can be shown in detail by computing the strain distribution for simple homogenous bodies, using Hertz contact theory (see e.g. [1]), or by computer simulations of complex finite-element models of the skin.

Tactile-flow induced illusions can be used in positive to address some of the technological difficulties arising in the development of haptic displays. The first such application involved the realization of a device displaying different CASR relationships, which can be used to increase the reliability of virtual or remote haptic perception of softness with respect to levels affordable by current technology.

6 Conclusions

In this paper, we investigated tactile illusions originated in the dynamic exploration of objects by the human fingertip. A strong resemblance to visual illusions generated by optic flow has been observed, which motivated us to introduce a notion of tactile flow. A computational model of tactile flow has been presented, which is consistent with, and explains most of the experimental results, while is amenable to some interesting engineering applications in the realization of haptic displays. Further studies are envisioned to better ground the hypothesis in the neurophysiology and psychophysics of touch, and to investigate a possible supramodality of flow perceptions across different sensorial channels.

References

1. A. Bicchi, D. De Rossi, E. P. Scilingo: The role of the contact area spread rate in haptic discrimination of softness. IEEE trans. on Robotics and Automation (2000) 16(5): 496-504.
2. R. Cipolla and A. Blake: Surface orientation and time to contact from image divergence and deformation. In G. Sandini, editor, Proc. 2nd European Conference on Computer Vision, pages 187-202, Santa Margherita, Italy, 1992. Springer-Verlag.
3. D. F. Collins, K. M. Refshauge, S. C. Gandevia: Sensory integration in the perception of movements at the human metacarpophalangeal joint. J Physiol (Lond) (2000) 529: 505-515.
4. M. J. Dodson, A. W. Goodwin, A. S. Browning, H. M. Gehring: Peripheral neural mechanisms determining the orientation of cylinders grasped by the digits. J Neurosci (1998) 18: 521-530.
5. C. J. Duffy, R. H. Wurtz: Sensitivity of MST neurons to optic flow stimuli. I. A continuum of response selectivity to large-field stimuli. J Neurofisiol (1991) 65: 1329-1345.
6. C. J. Duffy, R. H. Wurtz: Sensitivity of MST neurons to optic flow stimuli. II. Mechanisms of response selectivity revealed by small field stimuli. J Neurofisiol (1991) 65: 1346-1359.
7. N. Fisher, J. M. Zanker: The directional tuning of the barber-pole illusion. Perception 1001, volume 30, n.11, pp. 1321-1336.

8. J. J. Gibson: The perception of the visual world. Boston: Houghton Mifflin (1950)
9. M. S. Graziano, R. A. Andersen, R. Snowden: Tuning of MST neurons to spiral motions. J. Neurosci (1994) 124: 54-67.
10. J.D. Greenspan: "A Comparison of Force and Depth of Skin Indentation upon Psychophysical Functions of Tactile Intensity *Somatosensory Research*, Vol. 2, No. 1, 1984, pp. 33-48.
11. B. K. P. Horn and B. G. Schunck: Determining Optical Flow. AI 17 (1981): 185-203.
12. K. O. Johnson, T. Yoshioka, F. Vega Bermudez: Tactile functions of mechanoreceptive afferents innervating the hand. J Clin Neurophysiol (2000) 17: 538-558.
13. S. J. Lederman and R. L. Klatzky: “Sensing and displaying spatially distributed fingertip forces in haptic interfaces for teleoperator and virtual environment studies”, Presence, vol. 8, pp. 86-103, 1999.
14. V. G. Macefield, C. Hager-Ross, R. S. Johansson: Control of grip force during restraint of and object held between finger and thumb: response of cutaneous afferents from the digits. Exp Brain Res (1996) 108: 155-171.
15. M. C. Morrone, M. Tosetti, D. Monatanaro, A. Fiorentini, G. Cioni and D. C. Burr: A cortical area that responds specifically to optic flow, revealed by fMRI. Nature Neuroscience, Vol. 3 (2000) 12: 1322-1328.
16. H. Olausson, J. Wessberg, N. Kakuda: Tactile directional sensibility: peripheral neural mechanism in man. Brain Res (2000) 866: 178-187.
17. G. A. Orban, L. Lagae, A. Verri, S. Raiguel, D. Xiao, H. Maes, V. Torre: First-order analysis of optical flow in monkey brain. Proc Natl Acad Sci USA (1992) 89: 2595-2599.
18. J. R. Phillips, K. O. Johnson: Tactile spatial resolution: II. Neural representation of bars, edges and gratings in monkey primary afferents. J Neurophysiol (1981) 46: 1192-1203.
19. B. H., Jr. and L. M. Pubols: "Magnitude scaling of displacement and velocity of tactile stimuli applied to the human hand", *Brain Res.*, 233:409-413.
20. H. A. Saito, M. Yukie, K. Tanaka, K. Hikosaka, Y. Fukada, E. Iwai: Integration of direction signals of image motion in the superior temporal sulcus of the macaque monkey. J Neurosi (1986) 6: 145-157.
21. S. J. Schaafsma, J. Duysens, C. Gielen: Responses in ventral intraparietal area of awake macaque monkey to optic flow patterns corresponding to rotation of planes in depth can be explained by translations and expansion effects. Vis Neurosci (1997) 14: 633-646.
22. M. A. Srinivasan and R. H. LaMotte, "Tactile Discrimination of Softness",*Journal of Neurophysiology*, Vol. 73, No. 1, pp. 88-101, Jan 1995.
23. K. Tanaka, Y. Fukada, H. A. Saito: Underlying machanism of the response specificity of expansion/contraction and rotation cells in the dorsal part of the medial superior temporal area of the macaque monkey. J Neurosi (1989) 62: 642-656.
24. L. M. Vaina: Complex motion perception and its deficits. Current Opinion in Neurobiology (1998) 8: 494-502
25. F. Vega Bermudez, K. O. Johnson: SA1 and RA receptive fields, response variability and population responses mapped with a probe array. J Neurophysiol (1999) 81: 2701-2710.