Tactile Rivalry Demonstrated with an Ambiguous Apparent-Motion Quartet

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Summary

When observers view ambiguous visual stimuli, their perception will often alternate between the possible interpretations, a phenomenon termed perceptual rivalry [1]. To induce perceptual rivalry in the tactile domain, we developed a new tactile illusion, based on the visual apparent motion "quartet" [2]. Pairs of 200 ms vibrotactile stimuli were applied to the finger pad at intervals separated by 300 ms. The location of each successive stimulus pair alternated between the opposing diagonal corners of the ~1 cm² stimulation array. This stimulation sequence led all participants to report switches between the perception of motion traveling either up and down or left and right across their fingertip. Adaptation to tactile stimulation biased towards one direction caused subsequent ambiguous stimulation to be experienced in the opposing direction. In contrast, when consecutive trials of ambiguous stimulation were presented, motion was generally perceived in the direction consistent with the motion reported in the previous trial. Voluntary eye movements induced shifts in the tactile perception towards a motion axis aligned along a world-centered coordinate frame. Because the tactile quartet results in switching perceptual states despite unvaried sensory input, it is ideally suited to future studies of the neural processes associated with conscious tactile perception.

Results and Discussion

Rivalry in tactile apparent motion
In vision, the apparent-motion-quartet stimulus consists of pairs of dots alternately presented at the diagonal corners of an invisible square (Figure 1A) [2]. When viewing this stimulus, the dots will switch from appearing to jump either vertically or horizontally between the four corner locations (Figure 1B). To deliver an analogous sequence of vibrotactile pulses to the pad of the right index finger, we used the STReSS² tactile stimulator [3] consisting of a grid of piezoelectric tactors (Figure 1C and 1D). During stimulation with the "tactile quartet," participants were instructed to continuously report their perceptual experience by holding down one of two keys, corresponding to perceived motion along either the vertical or horizontal axis, respectively. Any time the tactile percept could not be categorized as either vertical or horizontal, participants were told to hold down both keys.

Within the first 2 min trial, all eight subjects reported perceptual switches between vertical and horizontal motion (inter-switch interval: $\mu = 31.9$ s, $\sigma = 14.6$ s). While this timing was slower than the 1–10 s switch interval generally reported for other forms of perceptual rivalry [4-6], it was comparable to the rate of switching reported by the same subjects during a 2 min trial of the visual quartet illusion. The dynamics of the tactile switching was consistent over subsequent retesting and was unaffected by observer's expectations or knowledge about the stimulation sequence provided. Surprisingly, the percept induced by the tactile quartet was generally described as resembling smooth motion across the finger tip, with participants unaware that only two discrete points were being stimulated at a time (additional details about the statistical analysis of the switch dynamics and the subjective reports are provided in the Supplementary Data). The reported perception of continuous motion is distinct from the perception of jumping between discrete locations that is generally reported for related tactile illusions such as the cutaneous rabbit [7, 8] and the visual apparent-motion quartet on which the current tactile illusion was based [2]. Extensive piloting from OC and TK found the experience of continuous motion to be robust across a variety of different stimulus parameters, though at reduced intervals the motion signal became degraded and turned into a diffuse buzzing sensation across finger tip. Future studies are needed to characterize the full range of spatial and temporal stimulation parameters capable of inducing bistable tactile apparent motion.

To our knowledge, this new tactile quartet illusion provides the first demonstration that ambiguous tactile stimulation can induce tactile rivalry with clear and regular switches between competing tactile perceptual states. These findings complement new research showing rivalry in the auditory domain [5] and provide strong evidence that perceptual rivalry may reflect a generalized strategy for dealing with perceptual ambiguity [9-11]. Although it is premature to speculate about the mechanisms underlying tactile rivalry, the demonstration of its existence provides new avenues to test and expand the computational and neurobiological models currently dominating vision science [1, 12].

Adaptation and perceptual biases
In audition and vision, adaptation paradigms have shown that prior exposure to a stimulus biased towards one of the rivalrous percepts will cause subsequent ambiguous stimulation to be dominated by the opponent perceptual interpretation [13, 14].

A **Visual quartet stimulus**

B

C **Tactile piezoelectronic stimulator**

D **Ambiguous tactile quartet**

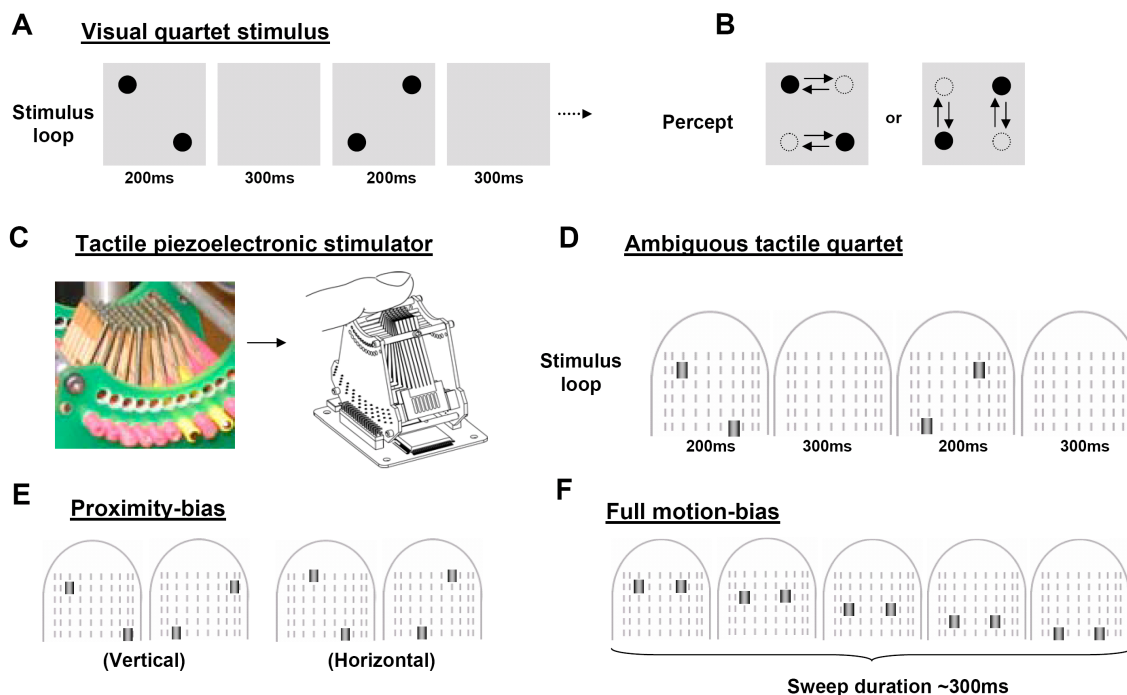**E** **Proximity-bias**

F **Full motion-bias**

Figure 1. Apparent motion stimuli.

(A) The visual quartet consists of a cycle of four stimulus frames. Two dots are presented at the diagonal corners of an invisible square on a uniform background. After a brief inter-stimulus interval, two dots of identical appearance are presented in the opposing corners.
(B) The dots will appear to jump between the two locations either vertically or horizontally (indicated by the black arrows).
(C) The device used to deliver tactile stimulation is composed of a grid of individually controlled piezoelectric tactors.
(D) The tactile quartet sequence involves pairs of 200 ms vibrotactile pulses applied to diagonally opposed regions of the finger pad, with each pulse pair separated by 300 ms of no stimulation.
(E) The vertical (left) or horizontal (right) separation of the stimulation regions was altered to bias the perception towards vertical or horizontal respectively.
(F) In experiment 2, the entire path of the motion sweep was sequentially stimulated in parallel between the respective top/bottom or left/right corners of the grid (a single downward sweep is illustrated).

We therefore sought to determine whether prior exposure to biased stimulation would have similar effects on tactile perception. Because dots in the visual quartet are perceived the vertical or horizontal distance between stimulation sites (Figure 1E and Experimental Procedures). Subjects were presented vertically biased, horizontally biased, or unbiased quartets for 20 s and then stimulated for 20 s with the unbiased ambiguous quartet (the adaptation period and subsequent test periods were separated by a 3 s pause). Each of the three adaptation-test pairs was presented consecutively, also separated by a 3 s pause.The subjects were unaware of the adaptation-test pairs and were told only that they would be presented with six 20 s blocks and were instructed to report their experience continuously as they had done in the initial 2 min trail. This sequence of six 20 s blocks was repeated three times throughout the experiment with the order of adaptation conditions counter-balanced within and across subjects.

Averaging across responses from all subjects, there was no significant difference between the perceived direction of tactile motion during 20 s of vertically- or horizontally-biased tactile stimulation (for full details of all statistical analysis see the Supplementary Data). Although no effect was found during the biasing period, there was evidence of significant adaptation away from the biased direction during the subsequent 20 s presentation of the ambiguous tactile quartet (Figure 2A). Because the proximity-bias did not consistently produce the expected percept, the effect of more extreme biasing was

explored in a second experiment involving a different sample of eight participants (see Experimental Procedures). Here, unambiguous sweeps of vertical or horizontal motion were produced by activating successive pins aligned along the parallel vertical or horizontal trajectories defined by the four stimulation sites used in the ambiguous apparent motion quartet (Figure 1F). The motion-sweep stimulus resulted in strong biasing with all participants consistently reporting motion in the direction consistent with the stimulus motion. During the 20 s of subsequent ambiguous stimulation, motion was significantly more likely to be reported in the opposite direction to the previous motion bias (Figure 2B). Together, these results show that adaptation to both subthreshold and clear motion sweeps biases ambiguous motion away from the adapted direction.

To assess the effect of previous perceptual experience (in the absence of any stimulus bias), we pooled the data from the 1/3 of trials in experiment 1 and 2 in which the ambiguous quartet was presented during both the adaptation and test periods. The data was then sorted depending on the dominant percept in the final 1 s of the adaptation period. This allows us to compare the ambiguous stimulation trials in which the previously dominant percept was vertical against trials previously dominated by horizontal. Interestingly, prior perceptual bias was found to significantly increase the likelihood that the same percept would remain dominant after the 3 s interval (Figure 2C).
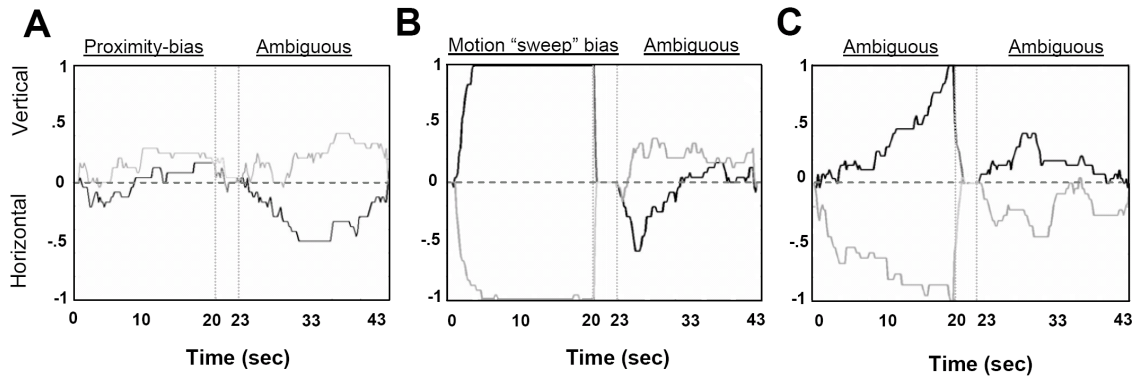
Figure 2. Average responses pooled across all subjects show the effect of vertical (black trace) and horizontal (gray trace) biasing. The y-axis shows predominance of vertical motion represented by positive values and horizontal motion by negative values

(A) No effect of biasing was evident during the 20 s segment of proximity-biased stimulation used in experiment 1. However, during the subsequently presented ambiguous stimulation, motion was more frequently perceived to travel along the axis orthogonal to the previous biased direction.
(B) In experiment 2, the motion sweep bias resulted in 100% dominance of perceived motion consistent with the stimulus. Despite the success of this biasing method, only a modest rebound effect was reported during the subsequent ambiguous quartet presentation.
(C) Data pooled across all non-biased ambiguous trials in experiment 1 and 2 was used to asses the effect of previous perceptual experience. Trials are divided into those in which the final 1 s of the initial ambiguous period was dominated by vertical (black line; n = 26) or horizontal (grey line; n = 22) motion. In the subsequent period of the ambiguous stimulation the percept was significantly more likely to be consistent with the prior percept.

The fact that the perception of ambiguous stimulation can be biased by adaptation to tactile motion provides evidence of a role for neurons tuned for the direction of tactile motion may be involved in determining the dominant percept in the tactile-quartet illusion. Beyond the demonstrated effects of adaptation, one interesting feature of these results is that the magnitude of the adaptation effect appears to be relatively weak and insensitive to the large difference in the success of the two biasing methods used. In contrast to the repulsive effect of adaptation to stimulus bias, our results suggest that previous perceptual experience has a facilitative effect on subsequent perceptual states in tactile perception. This stabilizing influence of prior perceptual experience is consistent with recent results in vision and audition [13, 16]. Like visual and auditory rivalry, this suggests that tactile rivalry may provide insights into the nature of perceptual memory and its influence in determining the contents of subsequent tactile awareness [13, 16, 17]. Aside from the scientific relevance of these findings, the fact that exposure to biased motion promotes dominance of the opposite percept, while exposure to ambiguous quartets facilitates dominance of the same percept, provides evidence against the existence of systematic response biases.

Crossmodal Effects of Visual Mental Imagery and Eye Movements
In the visual domain, eye movements, attention, and auxiliary visual cues are all known to interact with the perceived direction of apparent motion [15, 18]. It was also recently demonstrated that voluntary hand movements could influence perceptual dominance during visual rivalry [19]. Therefore, at the end of experiment 2, we included an additional set of conditions to explore the effects of eye movements and visual imagery on the perceived direction of motion during a 30 s presentation of the ambiguous tactile quartet. While performing one of seven different mental imagery or eye-movement tasks, subjects were instructed to count and verbally report the number of switches that occurred at the end of the trial (see Figure 3 for illustrations and descriptions of the seven experimental conditions). The number of switches reported during the 30 s were then compared against the average number of switches expected to occur on the basis of the switch rates calculated from the earlier 2 min presentations of the ambiguous tactile quartet (see Supplemental Data for a table of all relevant statistical details). Participants were instructed to close their eyes and make eye movements orthogonal to the perceived direction of the tactile motion. In the event that the perceived tactile motion direction switched, subjects were required to make the appropriate changes to the direction of eye movements. For all eight subjects, these eye movements significantly increased the number of tactile switches experienced. Imagery of motion had no effect, while imagery of orthogonally aligned stationary parallel lines resulted in a small but non significant increase in switch number (Figure 3, left three columns).

In the following four conditions we explored whether the observed relationship between eye movements and the perceived tactile motion direction could be attributed selectively to either local coordinate reference frames (retinotopic or somatotopic), or space-based frames. Participants were instructed to make eye movements while either their hand or their head was rotated 90° relative to their body. Local vertical motion was defined in the tactile domain as the axis aligned from the tip to the base of the finger and in the visual domain as the trajectory between the chin to the forehead. In respect to world-centered space, vertical motion was defined as the direction from the center of the body to the stimulator device. To make the instructions consistent across conditions, each experimental condition was described in respect to both local (eye or finger) and world-centered coordinates. When participants were asked to make eye movements in the direction opposite to motion on the finger pad (same direction in world-centered space), there was no change in the number of switches reported irrespective of whether the hand or the head was rotated 90°. In contrast, a significant increase in the number of perceptual switches was found when participants made eye movements in the same direction to the motion on the finger pad (opposite direction in world-centered coordinates), when either the hand or the head was rotated
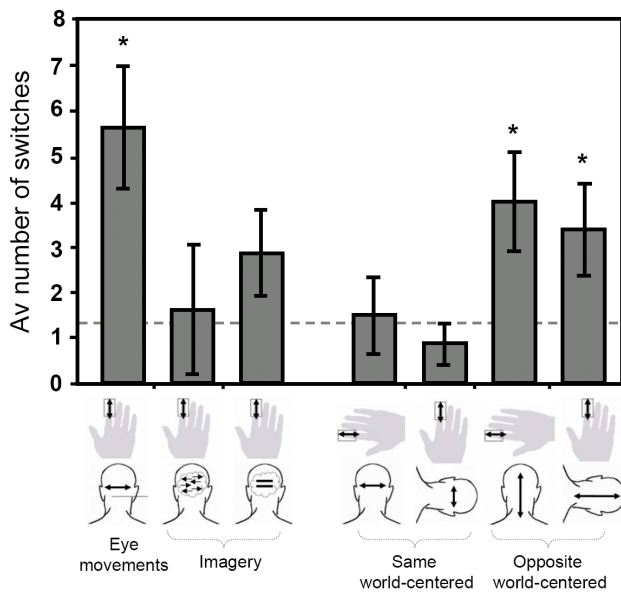
Figure 3. The effect of voluntary eye movements and mental imagery on the direction of perceived tactile motion.

The y axis indicates the average number of switches reported during 30 s of ambiguous tactile stimulation. Illustrated from left to right along the x axis, the first 3 bars correspond to the following participant instructions: (1) make large eye movements, (2) imagine parallel lines or (3) imagine visual motion in the *opposite* direction to that experienced in the tactile domain. In the event that the perceived tactile motion direction switched, subjects were required to make the appropriate changes to the direction of eye movements or imagery to maintain their orthogonal alignment. The remaining conditions assessed whether the effect of eye-movements were specific to local or space-based coordinate frames: (4) Rotate hand 90˚ or (5) rotate head 90˚ and make eye movements consistent with the tactile motion in world-centered coordinate space. (6) Rotate hand 90˚ or (7) rotate head 90˚and make eye movements in the opposite direction to the tactile motion along world-centered space. The grey dashed line indicates the number of switches expected on the basis of the mean switch rate observed during the initial 2 min presentation of the ambiguous tactile quartet for the same group of subjects. The asterisk denotes a significant ($p < 0.05$) difference from this expected switch rate. Error bars represent standard error of the mean.

90°. These results indicate that perceived tactile motion shows a strong bias to be consistent with the direction of eye movements in world-centered coordinate space (Figure 4, right four columns).

This influence of eye movements on tactile perception extends the scope of multi-modal interactions previously observed in visual rivalry [19]. Importantly, because the eyes were shut during the time, we believe the effects are likely related to the motor act itself and not the flow of visual motion across the retina. How and why eye movements are able execute their influence on tactile perception remains an open question. There are a number of cortical areas with overlapping tactile and visual representations that are potential candidates for these types of interactions including the superior colliculus [20] somatosensory area 2 [21], area VIP [22] and the MT+ complex [23, 24]. These multisensory areas may underlie a more abstract representation of motion shared across modalities, although further research is needed to investigate these crossmodal interactions.

Conclusions

This study provides the first demonstration that perceptual reversals can be induced by ambiguous tactile apparent motion. These results suggest that perceptual rivalry may be a strategy for resolving sensory ambiguity that is common to all modalities. Future comparisons between analogous tactile, visual, and auditory rivalry may help determine whether the similarities across sensory modalities extend to the mechanistic level. Because the perceptual switches generated by the tactile quartet involve shifts between orthogonal motion directions, this stimulus is particularly amenable to future electrophysiology and neuroimaging investigations of the neural processes involved in tactile awareness.

Experimental Procedures

Thirteen volunteers were recruited from Harvard University and Massachusetts Institute of Technology (eight male, five female; mean age 28.8 year, SD ±3.0). Apart from the authors (OC and TK), all participants were naïve to the aims of the experiment and were unfamiliar with the tactile stimulating device. Eight subjects participated in experiment 1 and 2 (four subjects participated in both experiments 1 and 2). Three subjects participated in two extended 10 min tests of the tactile and visual quartet. All experiments were approved by the Massachusetts Institute of Technology Committee On the Use of Humans as Experimental Subjects and conformed to guidelines of the Declaration of Helsinki.

Tactile stimuli were applied using the STReSS[2] distributed tactile stimulator [3]. The active area of the stimulator was 10.6×11.3 mm, composed of 60 piezoelectric actuators forming a 6×10 array of 'tactors' with spatial resolution of 1.8 by 1.2 mm. Each actuator could be independently driven to laterally deform the skin with maximum traction of 0.15 N allowing highly concentrated skin loading to be achieved by differential traction within a sub-millimetric area. Each actuator was independently controlled by custom developed software running on a Xenomai real-time system.

During the periods of ambiguous quartet stimulation, the 4 stimulation sites formed the corners of a square of 5×5 sites within the 6×10 grid. The stimulation sequence alternated between stimulation of each pair of diagonally opposing sites driven at a frequency of 80 Hz for a period of 200 ms.

In the biasing condition of experiment 1, the vertical and horizontal proximity-bias was achieved by programming the stimulus to span either a grid of 5×7, or 6×4 sites respectively. All other parameters were identical to those used in the ambiguous condition. In experiment 2, the biasing stimulus was achieved by activating, the 5 adjacent pins between each of the four corners of the ambiguous quartet. The pins would be activated sequentially, each for 56 ms resulting in a 280 ms sweeps along the wo corresponding vertical columns or horizontal rows of pins. After a silence period of 196 ms the pins were sequentially activated in the reverse order (simulating the sensation of motion returning back to the original locations).

Supplemental Data

Supplemental Data include Supplemental Results, Experimental Procedures, one figure, and five tables and can be found with this article online at
http://www.current-biology.com/cgi/content/full/18/14/1050/DC1/.

References

1. Blake, R., and Logothetis, N. (2002). Visual competition. Nat Rev Neurosci *3*, 13-21.
2. Ramachandran, V.S., and Anstis, S.M. (1985). Perceptual organization in multistable apparent motion. Perception *14*, 135-143.

3. Wang, Q., and Hayward, V. (2006). Compact, portable, modular, high-performance, distributed tactile transducer device based on lateral skin deformation. 14th Symposium on haptic interfaces for virtual environment and teleoperator systems IEEE VR, 67-72.

4. Brascamp, J.W., van Ee, R., Pestman, W.R., and van den Berg, A.V. (2005). Distrtibutions of alternation rates in various forms of bistable perception. JOV *5*, 287-298.

5. Pressnitzer, D., and Hupé, J. (2006). Temporal dynamics of auditory and visual bistability reveal common principles of perceptual organization. Curr Biol *16*, 1351-1357.

6. Carter, O.L., and Pettigrew, J.D. (2003). A Common Oscillator for perceptual Rivalries? Perception *32*, 295-305.

7. Geldard, F.A. (1982). Saltation in somesthesis. Psychol Bull *92*, 136-175.

8. Geldard, F.A., and Sherrick, C.E. (1972). The cutaneous "rabbit": a perceptual illusion. Science *178*, 178-179.

9. Andrews, T., and Purves, D. (1997). Similarities in normal and binocular rivalrous viewing. Proc Natl Acad Sci U S A *94*, 9905-9908.

10. Pettigrew, J. (2001). Searching for the switch: Neural bases for perceptual rivalry alternations. Brain and Mind *2*, 85-118.

11. Einhäuser, W., Stout, J., Koch, C., and Carter, O. (2008). Pupil dilation reflects perceptual selection and predicts subsequent stability in perceptual rivalry. Proc Natl Acad Sci U S A *195*, 1704-1709.

12. Tong, F., Meng, M., and Blake, R. (2006). Neural bases of binocular rivalry. Trends Cogn Sci *10*, 502-511.

13. Snyder, J., Carter, O., Hannon, E., and Alain, C. (In Press). Adaptation reveals multiple levels of representation in auditory stream segregation. J Exp Psychol: Hum Percept Perform.

14. Wolfe, J.M. (1984). Reversing ocular dominance and suppression in a single flash. Vision Res *24*, 471-478.

15. Ramachandran, V.S., and Anstis, S.M. (1983). Extrapolation of motion path in human visual perception. Vision Res *23*, 83-85.

16. Leopold, D.A., Wilke, M., Maier, A., and Logothetis, N.K. (2002). Stable perception of visually ambiguous patterns. Nat Neurosci *5*, 605-609.

17. Brascamp, J.W., Knapen, T.H., Kanai, R., Noest, A.J., van Ee, R., and van den Berg, A.V. (2008). Multi-timescale perceptual history resolves visual ambiguity. PLoS ONE *3*, e1497.

18. Madelain, L., and Krauzlis, R.J. (2003). Pursuit of the ineffable: perceptual and motor reversals during the tracking of apparent motion. J Vis *3*, 642-653.

19. Maruya, K., Yang, E., and Blake, R. (2007). Voluntary action influences visual competition. Psychol Sci *18*, 1090-1098.

20. Meredith, M.A. (2002). On the neuronal basis for multisensory convergence: a brief overview. Brain Res Cogn Brain Res *14*, 31-40.

21. Iwamura, Y. (1998). Hierarchical somatosensory processing. Curr Opin Neurobiol *8*, 522-528.

22. Duhamel, J.R., Colby, C.L., and Goldberg, M.E. (1998). Ventral intraparietal area of the macaque: congruent visual and somatic response properties. J Neurophysiol *79*, 126-136.

23. Hagen, M.C., Franzen, O., McGlone, F., Essick, G., Dancer, C., and Pardo, J.V. (2002). Tactile motion activates the human middle temporal/V5 (MT/V5) complex. Eur J Neurosci *16*, 957-964.

24. Beauchamp, M.S., Yasar, N.E., Kishan, N., and Ro, T. (2007). Human MST but not MT responds to tactile stimulation. J Neurosci *27*, 8261-8267.