The tactile speed aftereffect depends on the speed of adapting motion across the skin, rather than other spatio-temporal features

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Running head: Speed scaling of the tactile speed aftereffect

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Abstract
Following prolonged exposure to a surface moving across the skin, this felt movement appears slower, a phenomenon known as the tactile speed aftereffect (tSAE). We asked which feature of the adapting motion drives the tSAE: speed, the spacing between texture elements, or the frequency with which they cross the skin. After adapting to a ridged moving surface with one hand, participants compared the speed of test stimuli on adapted and unadapted hands. We used surfaces with different spatial periods (3, 6, 12 mm) that produced adapting motion with different combinations of adapting speed (20, 40, 80 mm/s) and temporal frequency (3.4, 6.7, 13.4 ridges/sec). The primary determinant of tSAE magnitude was speed of the adapting motion, not spatial period or temporal frequency. This suggests that adaptation occurs centrally, after speed has been computed from SP and TF, and/or that it reflects a speed cue independent of those features in the first place (e.g., indentation force). In a second experiment, we investigated the properties of the neural code for speed. Speed tuning predicts adaptation should be greatest for speeds at or near the adapting speed. However, the tSAE was always stronger when the adapting stimulus was faster (242 mm/s) than the test (30 – 143 mm/s), compared to when the adapting and test speeds were matched. These results give no indication of speed tuning, and instead suggest that adaptation occurs at a level where an intensive code dominates. In an intensive code, the faster the stimulus, the more the neurons fire.

Introduction
The tactile speed aftereffect (tSAE) is an illusory slowing of movement following a period of adaptation to motion across the skin (Stöber, reported in Rausch, 1960; McIntyre et al., 2012). For any given surface, temporal frequency (TF) - the rate at which texture elements move across the skin - increases with speed. The tSAE concerns
perceived speed, but it is not yet known whether it depends more on the speed of the
adapting stimulus, or more on its temporal frequency (TF).

Tactile primary afferents respond to periodic surfaces with action potentials
precisely phase-locked to the times the ridges cross their receptive fields (Darian-Smith
and Oke, 1980; Morley and Goodwin, 1987; McIntyre et al., 2012), i.e. the timing of the
spikes unambiguously signals the TF. These phase-locked responses involve bursts of
one or more action potentials for each ridge. Thus, the overall firing rate depends on
both the frequency of the bursts and the number of action potentials in the burst. The
firing rate is affected by changes in TF, speed, spatial period (SP; the centre-to-centre
distance between texture elements), and pressure (Goodwin and Morley, 1987).
Afferent spike rate is therefore ambiguous with respect to speed, and cortical processing
of peripheral inputs is required to isolate these features for perception.

In the cortex, the firing rate of some speed sensitive neurons in the primary
somatosensory area (SI) – especially areas 1 and 2 – reflects speed alone, being
insensitive to changes in SP, TF and pressure (Tremblay et al., 1996; Dépeault et al.,
2013). Thus, somewhere between the periphery and the speed-sensitive neurons in
areas 1 and 2, spatial and temporal frequency properties of the stimulus are combined
to produce a neural response dependent on a particular combination of those inputs -
speed - rather than their separate values. Therefore, by investigating whether the tSAE
depends on adaptation to speed, TF, and SP, we expected to learn something about
where in the stream of tactile processing the adaptation occurs.

Experiment 1 used psychophysical methods to test to what extent the tSAE was
based on changes induced by adaptation in the neurons sensitive to speed, TF and SP.
Multiple surfaces with different textures were used to disambiguate the effect of
adapting speed from adapting SP and TF. The results show that adaptation depends on
speed much more than on the other two features, which suggest the tSAE is caused by adaptation in areas 1 and 2 of S1, or beyond.

Little is known about speed coding in SI. Among the possible codes for speed are an intensive code and speed tuning, which both rely on firing rates. With an intensive code, a more intense - faster - stimulus evokes a stronger neural response. With speed tuning, distinct subpopulations of neurons respond most strongly to different speeds. The two codes might both occur at different levels of processing: for instance, speed tuning at one level may be followed by a level that encodes faster speed as a stronger neural response. Dépeault et al. (2013) characterized responses of SI neurons to speed, controlling for texture (spatial period). As mentioned above, they found speed-sensitive neurons in areas 1 and 2, but were "struck by the general lack of obvious speed tuning" (p. 1564). They found a monotonic increase in the mean firing rate with increases in speed from 40 – 100 mm s⁻¹, suggesting an intensive code for speed in this range. Other studies found a similar monotonic increase in response rates, testing with a broader range of speeds, from 32 - 350 mms⁻¹ (Whitsel et al., 1972, 1979; Collins and Roppolo, 1980; Tremblay et al., 1996).

Our Experiment 2 sought to distinguish between the possibility that speed is represented by an intensive speed code from the possibility that speed is represented by a speed-tuned code at the level where the adaptation causing the tSAE occurs. If neurons code speed intensively, the higher the speed of the stimulus, the more active the neurons will be. This greater activity will result in more adaptation for these neurons, causing them to respond less to any subsequent stimuli. This lesser response should yield a slower speed percept.

According to the speed tuning theory, different neurons prefer different speeds – that is, the speed that will maximally activate a neuron depends on the neuron. For higher speeds, some neurons may respond more, while others may respond less
A neuron tuned to a slow speed will adapt less to the faster speed than to slow speeds at or near its preferred speed. Generally, speed tuning predicts that when the adapting and test speeds are very different, the effect of adaptation on perceived speed will be small. In contrast, the intensive speed code predicts that faster speeds will have a greater effect even for slow tests.

**Method**

**Participants**

Twelve participants volunteered for the first experiment - ten naïve observers and two authors (labeled P01 and P04). Thirteen participants volunteered for the second experiment - ten naïve observers and the three authors (labeled P01, P03 and P05). Written informed consent was obtained and the Human Research Ethics Committee of the University of Sydney approved the study.

**Apparatus**

A variety of ridged hard rubber surfaces were attached to cylindrical drums. The ridges were 1 mm high. The ridge width was 1 mm for Experiment 1 and 10 mm for Experiment 2. The space between the ridges was varied in Experiment 1 (see Table 1), and was fixed at 12 mm in Experiment 2. The surfaces were covered with ladies’ stocking fabric (98% nylon, 2% elastine) to reduce friction with the fingers while the drums were in motion (without the covering, prolonged exposure to the moving drum was uncomfortable). The drums were rotated by two stepper motors (Lineartec MOT-122 High Torque Hybrid Stepping Motor) with a step size of 1.8 degrees controlled by LabView software (National Instruments, USA). At all speeds used, motion felt smooth and no vibration was detected from the stepper motor. A previous study using the same apparatus (McIntyre et al., 2012) validated this by showing that primary afferents...
responded in phase with the ridges passing the skin and were insensitive to the discrete steps of the motor.

When moving across the skin at threshold intensity, these surfaces, like most natural surfaces, may be expected to engage all types of primary afferents (Darian-Smith and Oke, 1980; Saal and Bensmaïa, 2014). The square-wave profile of the ridges is likely to include high frequency components at the onset and offset. As such, the surfaces more closely resemble pulsatile vibratory stimuli than sinusoidal, and each passage of a ridge should reliably evoke similar afferent responses over a wide range of temporal frequencies (Darian-Smith and Oke, 1980; Gardner and Palmer, 1989).

Procedure

Perceived speed was measured using the method of constant stimuli, with a 2-alternative forced choice task in which participants compared the speed of the drum felt with the adapted finger to that felt with the unadapted finger. The procedure is illustrated in Figure 1. Experimental sessions for adaptation conditions began with a 30-s adaptation phase, in which the reference finger was exposed to motion (the adapting stimulus). This was followed by the test phase, in which a speed presented to the reference finger was judged by comparing it to a stimulus presented on the other hand. Participants responded ‘left’ or ‘right’ to indicate which felt faster. The adaptation conditions also included 5 seconds of “top-up” adaptation following each left/right judgment. There was also a ‘no adaptation’ condition, in which perceived speed was measured for the test stimulus without any prior adaptation. This ‘no adaptation’ condition was used as a baseline.

Participants rested their arms on cushions, and were instructed to touch the drums with only the distal segment of the index finger. Only one finger was used to ensure that consistent pressure could be maintained. All stimuli moved in a proximal-to-distal direction. The standard stimulus was always presented to the adapted right finger. The
left finger was presented with a comparison stimulus. The comparison stimulus was presented with different speeds around that of the standard, to measure the point of subjective equality. These speeds were equally spaced on a logarithmic scale, and were chosen based on pilot data. White noise was delivered through headphones to mask the sound of the rotating drums, and vision of the textured surfaces was prevented with a cloth curtain.

The perceived speed of each standard stimulus was measured for each participant. It is given by the Point of Subjective Equality (PSE), the comparison speed at which the participant is equally likely to judge it is slower or faster than the standard stimulus. Logistic regression assessed the effect of log comparison speed on the responses. The 50% response point indicated by the regression was taken as the PSE.

Contact force

The contact force was measured with a scale under each drum. Participants were asked to maintain a constant pressure on the drums throughout the experiment. An auditory tone indicated when they pressed too hard (with a force greater than 0.39 N). In Experiment 2, an additional tone indicated when they pressed too softly (less than 0.10 N). This additional tone was not used in Experiment 1 because Experiment 1 involved the participants regularly lifting their fingers off the drums completely. The contact force data were analyzed to determine whether there was any systematic relationship between the experimental conditions and how hard the participants pressed on the surfaces; and also whether differences in contact forces applied by the two fingers affected speed judgments.

Experiment 1

Experiment 1 was conducted to determine whether the magnitude of the tSAE is higher for faster adapting stimuli purely due to their higher speed, or whether higher
temporal frequency (TF), or spatial period (SP) are also drivers of the effect. Given any two of these features, the third can be calculated (speed = SP × TF), meaning that at any one time, only two of the variables can be varied independently. Three laser-cut (0.15 mm tolerance) custom-made adapting surfaces (SP = 3, 6 and 12 mm) were used on the drums and presented at three speeds (20, 40 and 81 mms⁻¹) to produce three different TFs (3.4, 6.7 and 13.4 Hz). The combinations used are listed in Table 1. Each value of a given feature was tested with at least two different values of the other two features (e.g. 20 mms⁻¹ occurs with 3 mm, 6.7 Hz and also with 6 mm, 3.4 Hz).

The test stimulus was always the same (SP = 6 mm; speed= 40 mms⁻¹, TF = 6.7 Hz). The comparison stimulus was also 6 mm in SP but its speed varied between runs. Speeds around the standard stimulus were presented (12, 14, 19, 24, 32, 40, 52 and 68 mm s⁻¹), so that the point of subjective equality (PSE), which indicates perceived speed of the standard stimulus, could be measured.

The surface properties used were chosen from the range of stimuli that might be naturally encountered in the environment; the speeds used cover the range of functional scanning speeds (20 - 86 mm s⁻¹) spontaneously adopted during surface exploration (Connor et al., 1990; Smith et al., 2002; Yoshioka et al., 2007).

Table 1. The features of the adapting stimuli used in Experiment 1. Note that the "middle" adapting stimulus (denoted in bold) was identical to the test stimulus.

<table>
<thead>
<tr>
<th>Spatial Period (mm)</th>
<th>Speed (mms⁻¹)</th>
<th>Temporal Frequency (Hz)</th>
</tr>
</thead>
<tbody>
<tr>
<td>3</td>
<td>20</td>
<td>6.7</td>
</tr>
<tr>
<td>3</td>
<td>40</td>
<td>13.4</td>
</tr>
<tr>
<td>6</td>
<td>20</td>
<td>3.4</td>
</tr>
<tr>
<td><strong>6</strong></td>
<td><strong>40</strong></td>
<td><strong>6.7</strong></td>
</tr>
<tr>
<td>6</td>
<td>81</td>
<td>13.4</td>
</tr>
<tr>
<td>12</td>
<td>40</td>
<td>3.4</td>
</tr>
<tr>
<td>12</td>
<td>81</td>
<td>6.7</td>
</tr>
</tbody>
</table>
Because the adapting stimulus was sometimes a different spatial period than the test, participants had to move their finger from one surface during adaptation to another during test (Figure 2). To equate the finger movement across conditions, in all conditions participants were asked to move their finger to a second texture for the test. In the conditions involving the same SP for adaptation and test, the two textures were identical (see rightmost picture of Figure 2). Because the experiment also included top-up adaptation, participants were trained to move both fingers from one texture to the other every time the stimulus paused (in the No Adaptation condition, they moved their fingers, then moved them back immediately for the next test). The comparison finger was not subjected to any motion adaptation but nonetheless also alternated between two textures (of 6 mm SP).

The two textures required for a given finger in a condition were mounted side-by-side on a drum (Figure 2, Top). On one half of each surface was the standard stimulus texture (SP = 6 mm) used for the test, and on the other half was the adapting stimulus texture (SP = 3, 6 or 12 mm). A Plexiglas plate with two apertures was mounted in front of the drums. By becoming familiar with the size and feel of the apertures, participants quickly learned to switch their finger between the two apertures when the stimulus paused (Figure 2, Bottom).

All participants completed eight experimental sessions lasting 30 – 45 minutes each, one for each of the seven Adapting stimuli, plus the No Adaptation condition. These sessions were distributed across multiple days. The experiment was preceded by a brief practice to familiarize participants with the task. In each session, participants made 20 judgments for each of 6 comparison speeds, for a total of 960 trials over the course of the experiment. Each session consisted of four runs (two for the No Adaptation condition) separated by a 2-minute break. Each run for an adaptation condition began with the 30 s adaptation phase.
Experiment 2 was designed to test whether the tSAE was stronger when the adapting speed was faster, as predicted by intensive speed coding, or whether the tSAE would instead be strongest for particular adapting-test speed combinations as suggested by speed tuning. Four different test speeds were used: 30, 81, 143 and 242 mms$^{-1}$. For each test speed, participants were exposed to two adapting conditions. The 'faster' condition used an adapting speed (242 mm s$^{-1}$) that was faster than all but the fastest test speed. In the ‘matched’ condition, the adapting speed was the same as the test speed (for the 242 mm s$^{-1}$ test speed, there was only one adapting speed, labeled 'matched'). Two participants (P03 and P05) were tested in an additional adapting condition, 'slower' (30 mm s$^{-1}$). The conditions used in Experiment 2 are given in Table 2.

<table>
<thead>
<tr>
<th>Test speed (mm s$^{-1}$)</th>
<th>Adapting speed (mm s$^{-1}$)</th>
<th>Comparison speeds (mm s$^{-1}$)</th>
</tr>
</thead>
<tbody>
<tr>
<td>30</td>
<td>30</td>
<td>12, 15, 20, 24, 30, 39, 42, 47</td>
</tr>
<tr>
<td>81</td>
<td>30</td>
<td>34, 42, 52, 64, 81, 101, 127</td>
</tr>
<tr>
<td>144</td>
<td>30</td>
<td>59, 74, 91, 115, 144, 179, 225</td>
</tr>
<tr>
<td>242</td>
<td>30</td>
<td>100, 123, 155, 193, 242, 303, 377</td>
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<td>242</td>
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</table>
In Experiment 2, only one surface was required. This was the same surface as that used in a previous study (McIntyre et al., 2012). The ridges were spaced at regular intervals to produce a spatial period of 22 mm.

All participants completed eleven experimental sessions lasting 30 – 40 minutes each, one for each adapt-test speed combination, including the No Adaptation condition for each test speed (Figure 1). These sessions were distributed across multiple days. In each session, participants made 20 judgments for each of 7 comparison speeds in each of the 11 conditions, for a total of 1540 trials over the course of the experiment. There was a 2-minute break in the middle of each session, and the 30s adaptation phase was repeated when testing resumed.

**Results**

In both experiments, the tSAE was found: adaptation to motion resulted in a decrease in perceived speed of the test stimulus. Figures 3 and 4 show the psychometric functions for experiments 1 and 2, respectively. In Figure 3, the top row shows data for the No Adaptation condition, with the remaining rows showing data for increasing adapting speeds. The PSEs, indicated by the vertical lines, shift to the left as adapting speed increases, indicating that faster adapting speeds produce a stronger aftereffect. These common-speed curves cluster within each plot despite differences in TF and SP (indicated by plot symbol color and shape, respectively), pointing to adapting speed as the most important factor. Similarly, in Figure 4 there is a visible trend such that the lighter the curve (indicating a faster adapting speed), the further it is to the left (indicating a slower perceived speed). That is, the greater the adapting speed, the stronger the adaptation effect.
Features of the adapting stimulus (Experiment 1)

To assess and contrast the influence of the different features – speed, temporal frequency, and spatial period - PSE was plotted against each in Figure 5. Adapting speed appears to influence PSE such that greater adapting speeds produce a greater reduction in perceived speed (Figure 5A). In contrast, the plots of PSE against adapting SP and against adapting TF (Figure 5B and C) suggest these features have little effect on perceived speed.

The main purpose of this experiment was to assess how well each stimulus feature predicted the PSEs. This was quantified using a linear regression for each feature, done separately for each participant. Both the dependent variable (PSE) and the predicting feature were log-transformed. Adapting speed was a significant predictor of PSE for 10 of 12 participants. Adapting speed accounted for a mean of 70% (range: 43 to 96%) of the variance in PSE, with a mean slope of -0.29 (range -0.15 to -0.44). The slope of this log-log regression line is the exponent of the power function relating PSE to adapting speed.

In contrast to adapting speed, adapting SP and TF were significant predictors of PSE for only one participant each (P09 and P10 respectively), and in both cases, adapting speed accounted for more of the variance. The regression lines for the adapting speed model are illustrated in Figure 6. In order to test whether adapting speed was the sole significant predictor of PSE, separate models were tested with the addition of either adapting SP or adapting TF as predictors of PSE (ANOVA was used to compare models with and without the additional predictor). In only one case (P10) did either adapting SP or adapting TF significantly increase the explained variance beyond adapting speed alone.

The slopes of the psychometric functions (Figure 3) are an indication of speed discrimination sensitivity. Adaptation did not significantly change the slopes (F_{7,77} =
0.77, p = .612; repeated-measures ANOVA), suggesting that speed discrimination sensitivity was unaffected by adaptation. A previous study of the tSAE also found no effect of adaptation on sensitivity (McIntyre et al., 2012).

### Relative adapting speed (Experiment 2)

The purpose of Experiment 2 was to test whether an adapting speed faster than the test stimulus would produce a stronger tSAE than an adapting speed matched to the speed of the test stimulus. The results clearly showed that faster adapting speeds were associated with greater reductions in perceived speed (Figure 7). In 34 out of 39 cases (13 participants x 3 test speeds, 30, 81 and 144 mms⁻¹), the faster adapting stimulus produced a stronger tSAE than did adapting to the same speed as the test (Figure 7, right); also, the slower adapting speed produced a weaker tSAE in all 6 cases in which it was tested (2 participants x 3 test speeds 81, 144 and 242 mm s⁻¹). These results are consistent with an intensive code for speed, and no evidence of speed tuning was found.

To compare the magnitude of the tSAE for multiple test speeds, the proportion change in PSE from baseline was calculated for each adapting and test speed combination (Figure 7, left). When the adapting and test speeds were matched, the PSE was reduced by a mean (± 95% confidence interval) of 29 (± 2)% from baseline, very similar to the 30% reduction found in a previous study (McIntyre et al., 2012) and in Experiment 1, which found that when the adapting and test stimuli were both 40 mm s⁻¹, PSE was reduced by 30 ± 4% from baseline.

When the adapting speed was faster (242 mm s⁻¹) than the test speed (30-144 mm s⁻¹), the PSE was reduced by 43 ± 2% from baseline. This was significantly greater than the 29% reduction when adapting and test stimuli were matched (t₉⁹ = 4.5, p < 0.001; two-sample t-test). Again, this is consistent with Experiment 1, where when the adapting speed was faster (81 mm s⁻¹), PSE was reduced by 42 ± 4%. We also conducted an alternative analysis, a paired t-test, comparing the PSE for matched and faster
adapting speeds (with each pair having the same test speed and participant, see Figure 7, right). In order to do this, we had to exclude the matched condition in which both adapting and test speeds were 242 mm s\(^{-1}\) because there was no faster speed. This also revealed that adaptation with a faster speed produced a significantly greater reduction in perceived speed compared to adaptation with a matched speed (\(t_{38} = 6.9, p < 0.001, \text{mean difference} = 14 \pm 4\%\)).

Two participants were also tested with an adapting speed slower (30 mm s\(^{-1}\)) than the test speed (81 - 242 mm s\(^{-1}\), and the corresponding PSE was reduced by a mere 11 ± 3\% from baseline. Together with the results of the previous paragraph, this suggests that the faster the adapting speed, the greater the tSAE. This was also similar to the results in Experiment 1, which found that when the adapting speed was slower (20 mms\(^{-1}\)), PSE was reduced by a mean of 14 ± 5\% from baseline.

In contrast to these analyses of the proportional change of the test speed, the size of the aftereffect can alternatively be indexed by the absolute change in perceived speed in mms\(^{-1}\). The pattern of greater aftereffect magnitude for faster adapters than matched or slower adapters was the same. There was a difference in the relationship between test speed and the size of the aftereffect, in that the amount by which the test stimulus was underestimated following adaptation was greater for faster test speeds. This reflects the fact that perceived speed was reduced by similar proportional amounts for different test speeds.

Contact force

We analysed the contact force data recorded throughout the experiments. Figure 8 (left) shows the mean contact force for both left and right fingers, for the different experimental conditions in Experiment 1 (top) and Experiment 2 (bottom). In Experiment 1, the difference between contact force applied with each finger was not significantly related to adapting speed (\(F_{1,10} = 1.9, p = 0.201\)), nor to phase (adaptation vs.
test; $F_{1,10} = 0.3, p = 0.603$), nor was there a significant interaction effect ($F_{1,11} = 2.1, p = 0.176$), as revealed by a repeated-measures ANOVA. Similarly, in Experiment 2, the difference between the contact forces applied with each finger was not significantly different between any of the experimental conditions ($F_{13,123} = 0.7, p = 0.721$).

We also examined whether differences in contact force between the two fingers affected participants’ speed judgments. The top and bottom quartiles of the contact force difference data from individual trials across all participants and conditions of Experiment 1 were used to create two categories: 1) contact force is higher on the left (unadapted) finger, and 2) contact force is higher on the right (adapted) finger. The response data for all the trials falling into these two categories were pooled and plotted in Figure 8 (right). Unlike adapting speed, contact force discrepancy did not significantly affect participant responses ($F_{4968} = 0.4, p = 0.505$), nor did it significantly interact with comparison speed ($F_{4968} = 0.0, p = 0.980$), adapting speed ($F_{4968} = 0.3, p = 0.574$), or both ($F_{4968} = 0.2, p = 0.654$), as revealed by a one-way ANOVA.

**Discussion**

We found a large tSAE and determined that it depends on speed rather than temporal frequency or spatial period of the stimulus. Adaptation reduced perceived speed by between 11 and 43%, depending on the stimuli. When the adapting and test speeds are matched, perceived speed is reduced by approximately 30%. A previous report that found a similar aftereffect magnitude (McIntyre et al., 2012) used only matching adapting and test speeds. Here we found the tSAE was stronger when the adapting speed was faster than the test compared to when they matched. These results provide no evidence for speed tuning and support an intensive code for speed.
Cues for speed perception

Our results argue against a major role for spatial period and temporal frequency in speed adaptation. Nevertheless, speed judgments (without adaptation) are not entirely immune to the influence of one or perhaps both of these features. Dépeault et al. (2008) found a small but significant effect of spatial period on speed judgments: the surface with the highest SP (8 mm) was perceived as moving slower than surfaces with lower SP (accounting for 14-19% of the variance). This small discrepancy with the present findings may simply be due to different types of surfaces used (small raised dots instead of our ridges), or the method of measuring perceived speed (magnitude estimation instead of our forced choice paradigm).

We argue that tSAE reflects adaptation to speed and not some other stimulus feature. We have ruled out TF and SP. Primary afferents and S1 neurons additionally encode stimulus features associated with intensity. This raises the possibility that the tSAE is due to adaptation to intensity rather than speed. Intensity may be signaled in three ways. One way is the tangential force with which the ridges stretch the skin laterally. This rate of skin stretch may itself be a cue for speed (Seizova-Cajic et al., 2013).

A second, effect of speed is on the normal force with which surface features strike the skin (Dallmann et al., 2015). This potential cue for speed does not unambiguously signal absolute speed, but may do so in combination with other cues.

Thus, two features, one related to tangential and one to normal force, likely increased with greater stimulus speeds, and therefore may contribute to the adaptation

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1 Note that our measurements of contact force did not have sufficient temporal precision to distinguish force due to ridges and force at other times.
The contribution of these intensity-related speed cues is compatible with the conclusion that the speed encoded drives the adaptation. The third intensity cue is amplitude of indentation. However, our stimuli had constant amplitude (ridge height), and applied force did not vary systematically between the conditions, suggesting that this cannot account for our results. While perceived roughness increases with the height of surface features (Blake et al., 1997; Sutu et al., 2013), it is not clear whether ridge height would influence perceived speed. Further experiments would be needed to determine its influence on the tSAE.

**Neural site of adaptation**

The time between stimulation of two different points, combined with the distance between those points, is clearly a cue for speed (Pei and Bensmaïa, 2014). Less appreciated is that the features described in the previous section - skin stretch and amplitude of skin indentation - also vary with speed, and represent potential cues. Our finding that adapting speeds greater than the test cause greater adaptation suggests that the adaptation occurs in neural populations that code speed intensively, with firing rate increasing with speed over the range tested here (30 – 242 mms⁻¹). Of the cues mentioned above, our evidence for an intensive code seems more likely to reflect adaptation of intensity cues to speed than of the displacement over time cue. For the displacement over time cue, widely accepted models of visual motion perception expect speed tuning (Priebe et al., 2006; Bradley and Goyal, 2008), and expectations are similar for the coding of tactile motion (Pack and Bensaïa, 2015).

Both peripheral and central neurons adapt to intensity of stimulation and thus represent plausible sites that contributed to the adaptation underlying the tSAE. With regards to the central sites, our finding that speed rather than TF or SP drives the adaptation suggests central neurons sensitive to their particular combinations (speeds) as the adaptation site, rather than neurons that respond to independent variations in TF.
or SP in the range tested here (TF: 3.4 – 13.4 Hz and SP: 3 – 12 mm). For a number of
neurons in area 1 and 2, speed does seem to be a critical feature (Dépeault et al., 2013).
The responses of these neurons are unaffected by the TF (5 – 50 Hz) or SP (2 – 8 mm) of
the stimulus. Their firing rates increase monotonically with speed (40 – 100 mms⁻¹),
consistent with the intensive code for speed implicated by our psychophysical results.

The majority of individual SI speed-sensitive neurons cannot discriminate among
speeds as well as human perceptual judgments (Collins and Roppolo, 1980), and
Dépeault et al. (2013) suggested that higher order cortical areas may engage in
processing that determines perceived speed. The adaptation might involve those areas.

Neural coding of speed

We looked for one possible perceptual consequence of speed tuning: that test speeds
much faster than the adapting stimulus should yield a weaker aftereffect than when the
test and adapting stimulus are the same speed. This result did not occur, but its absence
does not rule out the possibility of speed tuning. If speed tuning were the neural code at
the site of adaptation, or another site affected by adapted neurons, the magnitude of the
tSAE would depend on factors including how many groups of neurons exist with each
responding to their own range of speeds (i.e. how many speed “channels” exist),
whether individual neurons respond to a broad or narrow range of speeds (i.e. how
broadly tuned they are), and how perceived speed is computed from the relative
responses within those separate speed channels (Schwartz et al., 2007). Under some
scenarios, a large difference in aftereffect would not occur with the conditions we tested,
and unfortunately with the limited neural evidence available, precise predictions cannot
be made about the tSAE under a speed tuning system.

The most parsimonious explanation of our results is an intensity code for speed: that
the adapted neurons signal higher speeds with higher discharge rates, because higher
adapting speeds uniformly led to stronger tSAEs. In contrast, speed tuning can result in
a non-monotonic relationship between adapting speed and tSAE strength, e.g. the adapting speed closest to the test speed producing the strongest aftereffects. Another potential outcome of speed tuning is perceived speed increasing after adaptation to a slower speed. This has been found in vision and been modeled as the result of adaptation on a population of speed-tuned neurons (Rapoport, 1964; Hietanen et al., 2008; Stocker and Simoncelli, 2009). Such perceptual repulsion away from an adapted value is fairly common across sensory modalities, occurring for example for perceived extent of limb movement (Seizova-Cajic et al., 2009), visual orientation (Clifford, 2014), and visual spatial frequency (Blakemore et al., 1970). But here we did not find evidence that adaptation to a stimulus slower than the test increased perceived speed (Figures 6 and 7).

Conclusion

We have found that surface speed is the primary determinant of tSAE. Neither the TF nor the SP of the adapting motion significantly influenced tSAE strength, suggesting that the phenomenon reflects adaptation at a level of the nervous system in which the speed of motion across the skin is coded by a cue independent of SP and TF, or at the level where speed has been computed from these two separate stimulus features. The latter is believed to be the case in areas 1 and 2 in SI (but not 3b), and may also occur in higher brain areas. We showed that higher adapting speeds produce a stronger aftereffect – larger reductions in perceived speed of the test. This is consistent with the action of an intensive code for speed.
Acknowledgments

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List of Figures

Figure 1. Experimental procedure. Illustration of the stimuli presented during adaptation, top-up and test. The adaptation conditions presented the adapting stimulus to the right index finger during the initial 30-s adaptation period and also in the 5-s top-up periods between tests. During the test phase, the standard stimulus was presented to the adapted right index finger and a comparison stimulus was presented to the unadapted left index finger. The baseline (no adaptation condition) had only the test phase.

Figure 2. Top: Representation of the surfaces used in Experiment 1. Each of the three pairs of surfaces pictured was mounted on its own drum. A fourth drum was used for the comparison stimuli, mounted with the right-most surface – 6 mm on both left and right. Unbeknownst to the participants, this surface had the same texture on both halves. Between blocks, the drums were swapped according to the adaptation condition. The spatial periods are given above each texture, with the ratio of ridge to gap width in brackets.

Bottom: During a run, participants switched the reference finger between the adapting texture (in this example, SP = 3 mm) and the standard texture (SP = 6 mm), guided by the aperture frame (grey). The comparison finger also switched apertures, even though the same texture was presented through both apertures (SP = 6 mm). The fingers are shown in position for the adaptation (and top-up) phase, in which the reference finger felt a moving surface, while the comparison finger felt a stationary surface. The arrows indicate where the fingers were placed during the test phase, when participants judged which finger’s surface moved faster.

Figure 3. Psychometric functions for each adaptation condition in Experiment 1. The ordinate shows the proportion of judgments for which the participant reported that the comparison speed was faster than the standard. This is plotted against comparison speed on a log-scale (standard stimulus: 40 mms⁻¹ speed; 6 mm SP; 6 Hz TF). The top row shows the baseline results (No Adaptation condition). The other rows show the psychometric functions following adaptation at 20, 40 and 81 mms⁻¹. Different colors indicate the adapting temporal frequency (red = 3.4, blue = 6.7, green = 13.4 Hz, and black = no adaptation), while different shapes indicate the adapting temporal frequency (square = 3, circle = 6, triangle = 12 mm, and cross = no adaptation). Vertical lines indicate the PSE for each condition, and can be compared across rows within a column (for the same participant). The line indicating the baseline PSE has been extended from the top row for easier comparison.
Figure 4. Psychometric functions for Experiment 2. For each participant (rows), different test speeds are shown in columns, and different adapting speeds are represented within each panel as separate lines, with lighter lines for higher speeds. On the ordinate is the proportion of trials that the participant judged the comparison speed to be faster than the standard (the test speed). On the abscissa is the comparison speed, on a log scale. Dotted lines show the Point of Subjective Equality (PSE) for each curve.

Figure 5. Points of Subjective Equality (PSE) obtained in Experiment 1, plotted in three different ways. The adapting stimulus has three important features (speed, TF and SP), and speed = SP x TF. The plots suggest that the strongest predictor of the tSAE magnitude is speed. PSE is re-plotted three times as a function of adapting speed (A), adapting SP (B) and adapting TF (C), on a log-log scale. In plot A, separate lines indicate the adapting SP (3, 6 and 12 mm); in plots B and C, separate lines indicate the adapting speed (20, 40 and 81 mms⁻¹). Separate data points are plotted for each participant, and lines indicate the group means.

Figure 6. Perceived speed following adaptation; individual data from Experiment 1. PSE is plotted as a function of adapting speed on a log-log scale. Error bars are the 95% bootstrapped confidence intervals (2000 samples). The dotted lines indicate the baseline PSE found with no adaptation, and solid lines are linear regression lines.

Figure 7. Left: proportion change in PSE for different adapting and test speed combinations, Experiment 2. Error bars are 95% confidence intervals of the mean (calculated between-subjects). Mean change in PSE is shown for each test speed following ‘slower’ (P03 and P05 only), ‘matched’, and ‘faster’ adaptation conditions. The negative scale means that lower values indicate a greater proportional decrease in perceived speed. Right: Individual data are shown for the difference in PSE for the ‘faster’ and ‘matched’ adapting speeds, for each of the three test speeds. The dashed line indicates the level of no difference between the PSE for the two adapting conditions. Most points lie below this line, indicating that a faster adapting speed resulted in lower perceived speed than a matched adapting speed did.

Figure 8. Left: Mean contact force, indicated by the weight of the finger on the apparatus, is shown for the two hands for each experimental condition for Experiment 1 (top) and Experiment 2 (bottom). Error bars are SDs (for the slow condition n = 2, so the individual data are shown). Right: Pooled participant responses are shown for the trials that had the greatest discrepancy between the contact forces applied by the two fingers (top and bottom quartiles).
Adaptation conditions

Adapting stimulus

Standard stimulus

Comparison stimulus

ADAPTATION & TOP-UP

TEST

Time

30s

5s 1s

on

off

adaptation

test

top-up

repeat

No adaptation condition

No adaptation condition

standard stimulus

Comparison stimulus

Time
stimulus felt during adaptation phase

REFERENCE FINGER

stationary during adaptation phase

COMPARISON FINGER

standard stimulus felt during test phase

comparison stimulus felt during test phase
Comparison Speed (mm s$^{-1}$)

Adapting TF (Hz)  
- 3.4  
- 6.7  
- 13.4  
- n/a

Spatial Period (mm)  
- 3  
- 6  
- 12  
- n/a
Comparison Speed (mm s\(^{-1}\))

Adapting Speed (mm s\(^{-1}\)): 0 \('<>\) 30 \('<>\) 81 \('<>\) 144 \('<>\) 242
Adapting Speed (mms$^{-1}$)

PSE (mms$^{-1}$)

Adapting TF (Hz)  
- 3.4 (red)
- 6.7 (blue)
- 13.4 (green)

Adapting SP (mm)  
- 3 (square)
- 6 (circle)
- 12 (triangle)
Adapting speed, relative to test speed

Proportional change in PSE

Test speed (mm s\(^{-1}\))

- 30
- 81
- 144
- 242

n = 2
n = 13

PSE\(_{\text{faster}}\) − PSE\(_{\text{matched}}\)
Experiment 1

Adaptation phase

Adaptation phase

Test phase

Test phase

Experiment 2

Test speed (mm s\(^{-1}\))

Test speed (mm s\(^{-1}\))

Contact force (grams)

Contact force (grams)

Adapting speed, relative to test

Adapting speed, relative to test

Contact force (grams)

Contact force (grams)

Comparison speed (mms\(^{-1}\))

Comparison speed (mms\(^{-1}\))

Adapting speed (mm s\(^{-1}\))

Adapting speed (mm s\(^{-1}\))

Proportion comparison faster

Proportion comparison faster

No adaptation

No adaptation

Adapted

Adapted

Adapted

Adapted