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Asymmetric interaction between motion and stereopsis revealed by concurrent adaptation

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14Although contingent aftereffects between motion and stereopsis have been referred to as behavioral evidence for the joint processing of the two features, the reciprocal nature of encoding the two features has not been systematically studied. 15Using a novel form of concurrent adaptation, we probed the perception of direction- and disparity-defined coherent surfaces 1617in parallel before and after adaptation to a stimulus that moved in a single direction at a particular binocular disparity. Contrary to earlier findings, we found a strong asymmetry between motion and stereopsis: the detection of disparity signal 1819 after adaptation was more impaired when the test stimulus was moving in the adapted direction than in the non-adapted direction, whereas the test disparity hardly affected the detection of coherent motion. However, motion adaptation became 2021dependent on disparity when we added another surface that was moving in the opposite direction at the opposite sign of disparity to those of the original adaptor, as in previous studies of contingent aftereffects. The observed asymmetric 2223contingency between motion and disparity adaptation urges the reinterpretation of previously reported contingent aftereffects and suggests a corresponding asymmetry between neural mechanisms devoted to processing of motion and stereopsis in 2425human visual cortex.

26 Keywords: motion, stereopsis, binocular disparity, adaptation, contingent aftereffects, joint processing

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Introduction

Motion and stereoscopic depth are two indispensable 3233 features for the localization of dynamic objects in threedimensional space and time. Computational algorithms for 3435processing these two features must resolve a common 36 problem, dubbed 'correspondence problem'. Optical inputs 37 must be matched across images in succession over time to register motion velocity. Similarly, the images from the 38 two eyes must be compared to encode stereoscopic depth. 3940 This commonality has been referred to as a theoretical ground for joint processing of motion and disparity (Qian 41 42& Andersen, 1997). The visual system indeed appears to benefit from joint processing of motion and disparity in 43numerous incidences. Motion and disparity information 44 help each other to integrate and segregate otherwise 45ambiguous signals (van Ee & Anderson, 2001; von 46 Grünau, Dube, & Kwas, 1993). The combination of the 4748 two features appears to be required to account for various perceptual phenomena or performances, including hyper 49stereoacuity for objects moving at high speed (Morgan & 50Castet, 1995), Pulfrich effects (Anzai, Ohzawa, & Freeman, 51522001; Qian & Andersen, 1997), and figure-ground segre-53gation (Bradley & Andersen, 1998; Bradley, Chang, &

Andersen, 1998). As neural substrates for joint processing54of direction and disparity, electrophysiological studies55have reported neurons tuned for both direction and disparity56in cats (Anzai et al., 2001) and in monkeys (DeAngelis57& Newsome, 1999; Grunewald & Skoumbourdis, 2004;58Pack, Born, & Livingstone, 2003; Roy, Komatzu, & 5959Wurtz, 1992).60

Psychophysical evidence for the presence of joint 61processing of motion and disparity came predominantly 62 from contingent aftereffects. A prolonged exposure to 63 two surfaces moving oppositely at different disparities 64 induced motion aftereffects (MAEs) in the direction 65opposite to that of motion paired with the given disparity 66 during adaptation (Anstis & Harris, 1974; Sohn & Seiffert, 67 2006; Verstraten, Verlinde, & Fredericksen, 1994). The 68 direction-contingent depth aftereffect was also reported 69 using Structure from Motion (SfM) stimuli (Nawrot & 70Blake, 1989, 1991). 71

Although these studies imply the presence of joint 72 processing, it does not provide detailed descriptions on 73 how motion and stereo information interact. In particular, 74 it is not clear how much of joint and non-joint mechanisms respectively contribute to the perception of stimuli 76 composed of the two features. Another related question 77 is whether the influences between the two features are 78

reciprocally balanced in terms of the magnitude and pro-79cessing precedence. To answer these questions, we carried 80 81 out psychophysical experiments employing a 'concurrent adaptation' procedure. Before and after adaptation to a 82 single stimulus defined jointly by direction and disparity 83 (Figure 1A), we probed the ability of observers to detect 84 85motion-defined and disparity-defined surfaces (Figures 1B and 1C). This protocol enabled us to assess the relative 86 contributions of the three potential mechanisms to the 87 88 processing of a stimulus jointly defined by direction and disparity: (1) direction-selective but disparity-nonselective, 89 (2) disparity-selective but direction-nonselective, and 90 (3) jointly selective to direction and disparity. We found a 91 strong asymmetry in contingent adaptation: disparity 92adaptation was highly dependent on motion information 93whereas motion adaptation was hardly affected by dis-94 95parity information.

Sohn & Lee

gg Materials and methods

99 Participants

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One of the authors and three naïve observers participated in *single-surface adaptation* experiments. Only three observers participated in the *stereo adaptation without motion* and *double-surface* experiments. All observers had normal or corrected-to-normal visual acuity and stereo vision. All participants gave written consent, approved by Seoul National University Ethics Committee.

108 Stimuli during adaptation

109Dichoptic stimuli were viewed through a mirror haploscope that was mounted on a head-chin rest to generate 110 stable perception of stereoscopic depth. As an adapting 111 stimulus, 110 white dots moving coherently in a single 112113direction (left or right) were randomly distributed within 114 an imaginary circular aperture of 2.48° radius against a black background. Dots were anti-aliased with subpixel 115resolution using a 2-D Gaussian filter with σ of .07°. The 116 maximum contrast of each dot was 100%. The stimulus 117 display was linearized using an 8-bit lookup table and the 118 mean luminance was 38 cd/m². In single-surface adapta-119*tion* experiments, all dots drifted at the same speed $(5^{\circ}/\text{sec})$ 120with an asynchronous, limited lifetime of 100 ms at the 121same depth plane (crossed or uncrossed disparity of 0.2°). 122Each dot disappeared after its own lifetime and then 123124 reappeared at a random position within the aperture. There were four adaptor types: leftward at front, rightward at 125front, leftward at far, and rightward at far. In the stereo 126adaptation without motion experiments, dots were iden-127tical to those in the concurrent adaptation experiments 128129except that dots remained stationary during the lifetime (static condition) or they moved in random directions 130

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А В Top-up adaptor (4 s) --Blank (.5 s) Tester 1 (.5 s) 4 Blank (.3 s) Tester 2 (.5 s) Time С Motion detection Stereo detection Task Task Task Task relevant -irrelevar elevant-irrelevant stereo stereo motion motion S S S S C S D D S D S S D Ċ

Figure 1. Schematic diagrams of experimental stimuli and conditions. A: Observers adapted to moving dots at crossed or uncrossed disparity (Leftward motion at crossed is shown). In the actual stimulus, white dots were presented against black background. At the center fixation point, a box containing segmented horizontal lines was presented for the gap detection task. The gap in the bottom line is shown here. B: An example of a single trial for motion detection. C: Test stimuli and conditions. Four test stimuli are shown. For simplicity, each tester is drawn as containing 100% coherence both for motion and depth. The label of each condition is shown under the table in the right side. The first and second letters in the condition name indicate whether the task-relevant and task-irrelevant features, respectively, are the same as the adaptor. 'SS': both features are the same as the adaptor (leftward at crossed). 'SD': task-relevant feature is the same as the adaptor but task-irrelevant is not. 'DS': task-relevant feature is different from the adaptor but task-irrelevant is the same. 'DD': both features are different from the adaptor.

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(random motion condition). In the *double-surface adapta-* 131 *tion* experiment, 110 dots were placed at a crossed disparity 132 of 0.2° and the other 110 dots at an uncrossed disparity of 133 134 0.2°. The two groups of dots moved oppositely, one to the135 left and the other to the right.

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137 Stimuli during tests

The dots were identical to the adapting dots except for 138contrast. The maximum contrast of each dot was $\sim 1\%$ for 139the low contrast condition and $\sim 3\%$ for the high contrast 140 condition (marked gray and black symbols, respectively, in 141 Figures 2, 3, 5, and 6). Two brief intervals were sequen-142tially presented during the test, the noise and the signal. In 143the motion detection sessions, all dots were presented at 144 145the same disparity as the adapting stimulus or at the same amount of disparity with the opposite sign. The signal 146interval contained coherent dots moving in a single direc-147148tion and noise dots moving in random directions, whereas the noise interval contained only randomly moving dots. 149All dots in the test stimulus for stereo detection were 150moving in a single direction identical or opposite to the 151adaptor. The noise interval contained only noise dots whose 152depths were scattered randomly over the disparity range of 153 -0.3° to $+0.3^{\circ}$. In the signal interval, coherent dots, which 154were located at a single disparity of either $+0.2^{\circ}$ or -0.2° , 155were embedded in noise dots. Since coherent dots were 156placed within the depth range of noise dots and spatially 157scattered in a 2-dimensional space, observers could not 158perform the task by simply detecting a few dots placed 159at the closest or farthest depth and were forced to 160identify a coherent, global depth plane amid the cloud of 161162noise dots. The particular range of disparity (-0.3°) to $+0.3^{\circ}$) was chosen carefully by conducting a pilot experi-163164ment, where we confirmed that observers were able to reliably detect a 100 % coherent depth plane with the 165duration of 0.5 seconds. We used four types of testers, 166 which differed in terms of whether their task-relevant 167and task-irrelevant features matched those of the adaptor 168 (Figure 1C). In the first type, both the task-relevant and 169task-irrelevant features were the same as the adaptor 170('SS' in Figure 1C). In the second, the task-relevant 171feature was the same as the adaptor but the other feature 172was not ('SD' in Figure 1C). In the third, the task-relevant 173174feature was different from the adaptor but the taskirrelevant one was the same ('DS' in Figure 1C). In the 175last, both features were different from those of the adaptor 176177('DD' in Figure 1C).

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179 **Experimental procedures**

An experimental session consisted of four pre- and postadaptation blocks. Each block contained 28 trials (seven levels of coherence × four test conditions: 'SS', 'SD', 'DS', and 'DD'). In pre-adaptation blocks, observers viewed two intervals of test stimuli and reported which interval contained coherent motion or disparity signal by pressing one of two keys (2 IFC). Each stimulus interval 186 lasted for 500 ms, and the inter-stimulus interval (ISI) was 187 300 ms (Figure 1B). The inter-trial interval was 1500 ms, 188 during which observers had to make a response. Post-189adaptation blocks started with a 40 sec of initial adaptation, 190and 4 s of top-up adaptation preceded each test trial. To 191ensure the stability of fixation and promote accurate 192binocular alignment of the two eyes during adaptation, we 193employed a 'gap detection' task (Sohn & Seiffert, 2006). In 194the initial adaptation, every 4 sec, a lined box appeared for 195500 ms around the fixation point (the enlarged inset in 196Figure 1A). Each horizontal line was broken into four 197segments, two of which were randomly selected to be 198 presented to one eye and the other two to the other eye. 199 There was always one segment missing either in the upper 200or in the bottom lines. Observers performed a one-back 201 task by reporting whether the position of the present gap 202was the same as the position of the gap that appeared 4 sec 203ago. During top-up adaptation, the box appeared at 1.5 sec 204and at 3.5 sec from the start of the stimulus. Observers 205reported whether the position of the gap was the same 206between the first and the second boxes. After adaptation, 2070.5 sec of blank screen with a fixation point was presented 208before the test stimulus appeared. 209

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Data analysis

Thresholds in different viewing conditions were sepa-212rately estimated using a hybrid technique, in which a 213constant stimuli method was applied within a session and a 214staircase method between sessions. In the starting session, 215the proportion of coherent dots in the signal interval varied 216across seven different levels, which was chosen out of a 217predetermined set of 30 coherence levels. In the following 218three sessions, based on the performance after each session, 219 we continued to adjust the range of coherence levels within 220the predetermined set such that the average percent correct 221was roughly around 75%. We obtained a psychometric 222curve from four sessions of data for each viewing condition 223and estimated a coherence threshold for 75% performance 224by fitting the cumulative Gaussian function to the curve. 225We repeated this procedure 1000 times by re-generating the 226data sets using a bootstrap method (Efron & Tibshirani, 227 1986), and obtained the mean threshold and an estimation 228error (SE). We performed this procedure for pre- and post 229adaptation conditions at each tester type, adaptor type, and 230 contrast level in each observer. Then, we calculated 231adaptation index (AI) defined below. 232

Adaptation Index (AI) =
$$\frac{(TH_{post} - TH_{pre})}{(TH_{post} + TH_{pre})}$$
, (1)

where TH_{pre} and TH_{post} indicate thresholds estimated 233 before and after adaptation, respectively. An AI can have 235



Figure 2. Detection thresholds and adaptation effects in the motion task. Data from different adaptor types, contrast levels of testers, and observers are plotted together. The shapes of symbols indicate different types of adaptor: RN for the adaptor moving to the rightward at the near disparity; LN for moving leftward at near disparity, RF for moving rightward at far disparity, and LF for moving leftward at far disparity. The brightness of symbols indicates the contrast level of tester stimuli: black for high contrast and gray for low contrast. A–D. Pairs of pre- and post-adaptation detection thresholds for four different tester conditions: A, same direction and same disparity as the adaptor ('SS'); B, different direction and same disparity ('DS'); C, same direction and different disparity ('SD'); D, different direction and different disparity ('DD'). The arrows and numbers indicate average thresholds for pre- and post-adaptation in each condition. E–F. Adaptation indices for the non-adapted disparity (ordinate) plotted against those for the adapted disparity (abscissa): E, Als from the condition where the test direction was the same as the adaptor; F, Als from the condition where it was opposite to the direction of the adaptor. The histograms are projected frequency distributions of Als along horizontal ('SS') or 'DS') or vertical axes ('SD' or 'DD'). High and low contrast conditions are described as stacked bars, each corresponds to black and gray portions of the bars. The bars in color indicate Als that were significantly different from zero with the 95% confidence interval of estimation (red for 'conventional adaptation' and blue for 'null adaptation'). The arrow indicates the average of the distribution. Error bars are standard error (SE) estimated by a bootstrap procedure (see Materials and methods).



Figure 3. Detection thresholds and adaptation effects in the stereo task. Figure formats and notations are the same as in Figure 2. A–D: Plots of 75% detection thresholds for disparity. Each plot represents four different experimental conditions, A: same disparity and same direction as the adaptor ('SS'). B: different disparity and same direction ('DS'). C: same disparity and different direction ('SD'). D: different disparity and same direction indices for the same (E) and different (F) disparities.

a value between negative one and positive one. A positive 236AI indicates an increase in detection thresholds after 237238adaptation and a negative means decreased thresholds. In this study, we call the latter type of adaptation 'null 239adaptation', as opposed to the conventional adaptation 240effects characterized by increased detection thresholds 241for the adapted feature. In order to evaluate the contingency 242243of adaptation on the task-irrelevant feature information, we normalized the difference between AIs from testers with 244

the adapted and non-adapted irrelevant features, and named 245 it contingency index (CI). 246

Contingency Index (CI) =
$$\frac{(AI_{same} - AI_{diff})}{\sqrt{\frac{SE_{same}^2 + SE_{diff}^2}{2}}}$$
, (2)

where AI_{same} is the AI from the condition where the taskirrelevant feature was the same as the adaptor and AI_{diff} is 249 250the AI from the test condition where the task-irrelevant feature was different from the adaptor. SE is standard error 251of estimation for each condition. A positive CI indicates 252253that an AI is greater when the tester contained the taskirrelevant feature that was presented during adaptation 254than when it contained non-adapted feature. A negative 255256CI means the opposite, and a CI near zero means no contingency between the two features. $257 \\ 258$

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260 Results

In the current study, following adaptation to an identical 262263adaptor defined by direction and disparity, we measured the detection performance for the direction-defined and 264disparity-defined coherent surfaces. Note that the motion 265and stereopsis tasks share the identical task structure 266('discriminating a surface of coherent signals from noise') 267and were both performed before and after adaptation, 268allowing direct comparisons between perceptual changes 269in the two features after adaptation. For quantitative 270comparison, we normalized the amount and the sign of 271272adaptation effects across conditions by computing adaptation index (AI) for each pair of pre- and post-adaptation 273274thresholds. A positive AI indicates an increase in detection thresholds after adaptation (conventional adaptation) and a 275negative means a decrease (null adaptation). We obtained 276thresholds at more than one level of test contrast (marked as 277black and gray symbols in Figures 2, 3, 5, and 6) because 278adaptation effects might vary in magnitude depending on 279280the contrast of test stimuli due to changes in contrast gain (Kohn & Movshon, 2003). Since we did not find any sys-281tematic difference between the results at different contrast 282levels, we merged results from different contrast condi-283tions for statistical tests. 284

285 Single surface adaptation: Little disparity 286 contingency in direction-selective adaptation

287In each tester condition, we obtained a total of 19 pairs of motion detection thresholds from pre- and post-adaptation 288conditions from four different observers. When the target 289direction was the same as the adaptor, motion detection 290threshold substantially increased (p < .05 for Wilcoxon's 291292matched pairs test) following adaptation regardless of 293whether the disparity of the tester, which was irrelevant to the motion detection, was the same as that of the adaptor 294('SS', Figure 2A) or not ('SD', Figure 2C). When these 295elevations in detection threshold were translated into AIs, 296the mean AI did not significantly differ between 'SS' (.13) 297298and 'SD' (.11) conditions (p = .69 for Wilcoxon's matched pairs test, Figure 2E). When the target direction 299was opposite to that of the adaptor, there was a tendency 300 that detection threshold decreased following adaptation 301

(note the data points under the diagonal line in Figures 2B 302 and 2D), indicating the presence of null adaptation. The 303 average AIs from the 'DS' (-.05) and 'DD' (-.07)304conditions were negative and were not significantly 305different from each other (p = .15 for Wilcoxon's matched 306 pairs test, Figure 2F). The overall trend of positive AIs 307 for the adapted direction and negative AIs for the direction 308 opposite to the adaptor was consistently observed in the 309 data from individual observers (Supplementary Figure 1A). 310

We evaluated the contingency of motion adaptation on 311 the task-irrelevant disparity information by comparing 312adaptation effects from the testers presented at the adapted 313 disparity and those from the testers at the non-adapted 314disparity. In doing so, we normalized the difference 315between AIs by taking into account their estimation error 316and named it contingency index (CI). (see Materials and 317 methods). CI provides a robust means to assess the mag-318 nitude and reliability of observed differences in adaptation 319effects especially when the size of adaptation substantially 320 varies across different adaptors or observers as in our data. 321 A positive CI indicates that an AI is greater at the adapted 322disparity than at the non-adapted disparity, a negative CI 323 means the opposite, and a CI near zero means no con-324 tingency between the two features. We plotted CIs against 325the pooled AI of the two disparity conditions in Figures 6A 326 and 6B, respectively for adapted (average CI = .32) and 327non-adapted directions (average CI = .44). The average 328 CIs were not significantly different from zero (p = .49)329 and .09 for Wilcoxon's signed rank test), meaning no 330 contingency in motion adaptation on disparity. None of 331 the AI pairs from the two disparity conditions was sig-332 nificantly different from each other in the adapted direction 333 and only one (out of nineteen) showed significant difference 334 (marked as red in Figure 6B) in the non-adapted direction. 335This lack of disparity contingency of motion adaptation 336 was not relevant to the size of adaptation effect, which 337 was indicated by no significant correlation between the 338 pooled AI and the magnitude of CI (r = .11 and .32 for 339 adapted and non-adapted directions. p > .05 for both 340conditions). The results indicate that in motion adaptation, 341there is no or negligible, if any, contingency on disparity. 342 343

Single surface adaptation: Strong direction 344 contingency in disparity-selective adaptation 345

Figures 3A–3D show stereo detection thresholds from 346 pre- and post-adaptation conditions for each of the four 347 tester conditions. When both the disparity and direction of 348 the tester were the same as those of the adaptor, the 349detection threshold increased after adaptation ('SS', 350Figure 3A; p < .01 for Wilcoxon's matched pairs test). 351In contrast, when the same disparity target was moving in 352the opposite direction to the adaptor, the thresholds sig-353 nificantly decreased ('SD', Figure 3C; p < .05 for 354Wilcoxon's matched pairs test). The similar tendency 355was observed when the test disparity was different from 356

357 that of the adapting stimulus; conventional adaptation effects shown as increased detection thresholds following 358 adaptation to the stimulus in the adapted direction ('DS', 359360 Figure 3B; p < .01 for Wilcoxon's matched pairs test) and null adaptation shown as decreased detection thresholds 361to the non-adapted direction ('DD', Figure 3D; p < .05362 for Wilcoxon's matched pairs test). Note that regardless of 363 the target disparity during the test, the sign of adaptation 364 was determined completely by whether the direction of 365366 the tester matched to that of the adaptor, even though the tester direction was irrelevant to the task here. Such data 367 patterns are shown as positive AIs with the adapted direc-368 tion (mean AI = .09 for 'SS' in Figure 3E; mean AI = .07369 for 'DS' in Figure 3F) and negative AIs with the non-370 adapted direction (mean AI = -.06 for 'SD' in Figure 3E; 371372 mean AI = -.05 for 'DD' in Figure 3F). This strong tendency of direction-dependent disparity adaptation was 373 consistent across individual observers (Supplementary 374Figure 1B) and confirmed by the positive average CIs 375for both the adapted (3.35, Figure 6C) and non-adapted 376 (2.72, Figure 6D) disparities (p < .01 for Wilcoxon's 377 signed rank test). For both disparity conditions, in nearly 378 50% of the AI pairs (9 out of 19), the AI from the tester 379 380 moving in the adapted direction was significantly larger than that from the tester in the opposite direction (marked 381as red in Figures 6C and 6D). The direction contingency 382of disparity adaptation became more pronounced as the 383 size of AI increased, evidenced by the high positive corre-384lation between AIs and CIs (r = .89 and .82 for adapted and 385 non-adapted disparity conditions. p < .01). This indicates 386 that the contingency was reliably observed whenever sub-387 stantially large adaptation was generated by a given adaptor. 388From these results, we conclude that the stereo detection 389 was impaired with the adapted direction and improved with 390 the opposite direction, regardless of the target disparity to 391392 be detected. 393

Robust disparity-selective adaptationwithout coherent motion signal

The results of the first two experiments showed that 396 397 direction-selective adaptation did not depend on the 398 disparity of adapting stimuli, whereas disparity-selective 399 adaptation was contingent upon the direction of adapting stimuli. While this asymmetry may be taken as the inherent 400 precedence of motion over stereo information processing, 401 an alternative explanation can account for the observed 402 asymmetry. Suppose that the adapting stimulus used in our 403study failed to induce substantial disparity adaptation and 404 was optimal only for generating motion adaptation. Then, 405the performance in either the motion or stereo task would 406 be hardly affected by the disparity of testing stimuli as 407observed in our data. 408

To exclude the possibility that our findings of asymmetric contingent adaptations were simply caused by the lack of disparity adaptation, we conducted a control 411 experiment. We repeated the stereo detection experiment 412 using adapting and test stimuli defined only by binocular 413disparity without any coherent motion signal. Since the 414 adaptor lacking coherent motion signal cannot generate 415direction-selective adaptation, any changes in detection 416 threshold occurring after adaptation should be attributed to 417 disparity adaptation. The three out of four observers in the 418 first two experiments participated. The stimuli and proce-419dure were exactly the same as those in the 'stereo detection' 420 experiment except how the positions of dots were updated 421over time. In the 'static' condition, dots remained sta-422 tionary for 100 ms, which was the same limited lifetime 423 as that in the concurrent adaptation experiments, and then 424 reappeared in a random position inside the circular 425display. Such stimuli elicit the percept of asynchronously 426twinkling dots without carrying any coherent motion. In 427the 'random motion' condition, each dot moved with the 428 same lifetime and speed as before. However, the directions 429of dots were equally spread over 360 degrees, and each dot 430 maintained its direction throughout the lifetime. In both 431 conditions, adaptation elevated detection thresholds for the 432adapted disparity (Wilcoxon's matched pairs test, p < .05; 433left two bars in Figures 4A and 4C) but did not generate 434any significant difference in thresholds for the non-435adapted disparity (p = .06 for both conditions; right two 436 bars in Figures 4A and 4C). Conventional adaptation 437 effects (positive AI) were evident for the adapted disparity 438(white bars in Figures 4B and 4D), and the sizes of 439disparity-selective AIs were not significantly different 440 from those for 'SS' condition of concurrent adaptation 441 (in both 'static' and 'random motion' conditions, p > .05442 for Wilcoxon's matched pairs test across three observers). 443

The considerable amount of disparity-selective adapta-444 tion makes the possibility unlikely that our adapting stimuli 445were not optimal enough to promote strong disparity adap-446 tation per se. Furthermore, considerable null adaptation 447 (negative AI) was observed for the non-adapted disparity 448 (gray bars in Figures 4B and 4D). These results undoubt-449edly indicate that disparity signals in our stimuli were by 450themselves strong enough to readily promote adaptation, 451but became limited as an adaptor when presented in 452conjunction with coherent motion signal. 453

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Double surface adaptation: Disparity455contingency in direction-selective adaptation456

While our finding of the direction dependency in stereo 457detection following concurrent adaptation is consistent 458with the previous studies that showed direction-contingent 459depth aftereffects in SfM stimuli (Nawrot & Blake, 1989, 460 1991), little stereo dependency in motion detection is rather 461 perplexing given previous studies that reported signifi-462 cant disparity-contingent directional aftereffects (Anstis 463& Harris, 1974; Sohn & Seiffert, 2006; Verstraten et al., 464



Figure 4. Stereo adaptation without coherent motion signal. A and C: Average thresholds for 75% performance in stereo detection before (white bars) and after (gray bars) adaptation: A for the static condition and C for the random motion condition. The error bars indicate standard error (SE) of the mean across different adaptors (at near or far disparity) and three observers. The asterisk indicates statistically significant difference between pre- and post-adaptation thresholds: p < .05 for Wilcoxon's matched pairs test. B and D: Average adaptation indices from three observers are shown for stereo adaptation with static (B) and with random motion (D). White bars are Als from the conditions where the tester disparity was the same as the adapting disparity and gray bars are when the target disparity was different from the adaptor. Error bars indicate SE estimated by a bootstrap.

1994). One notable difference between these studies and 465the current study is that the previous studies employed two 466 oppositely moving surfaces at different disparities as an 467 adaptor. We conjectured that such coexistence of double 468 opposing surfaces abolishes disparity-independent motion 469470 adaptation and selectively promotes disparity-contingent motion adaptation. Since adaptation by disparity-independent 471motion mechanisms would be cancelled between oppos-472ing directions in such an adaptor, only adaptation by the 473motion mechanism that is also tuned for disparity would 474475 be observed. On the other hand, in the adapting stimuli 476 consisting of a single surface like the one used in our study, since there is no potential suppression or cancellation 477 between opposing stimulus features, both types of adapta-478tion would be observed and the contribution of the jointly 479tuned mechanism would be relatively minimal. 480

481 Our interpretation led us to two predictions with the
482 addition of a double-opposing surface to our original adaptor:
483 first, direction-selective adaptation will be more contingent
484 on disparity, and, second, the size of direction-selective

adaptation itself will be reduced because the added surface 485cancels out opposite directional adaptation. We repeated 486 the motion detection experiment, but this time with two 487 adapting surfaces placed on top of each other. The adapting 488 stimulus contained two groups of dots that were moving 489oppositely at crossed and uncrossed disparities, respec-490tively. Test stimuli were the same as those in the experi-491ment with a single-surface adaptor. Note that, since both 492the two values of direction and disparity in test stimuli were 493presented as the adaptor, the condition where the test 494direction was non-adapted ('DS' and 'DD') did not exist. 495Thus, we categorized four types of test stimuli into two 496 conditions, 'SS' and 'SD'. For example, when the adaptor 497 was a leftward motion at crossed and rightward at uncrossed 498disparities, the 'SS' condition includes test stimuli with 499leftward motion at the crossed disparity and rightward at 500the uncrossed. Rightward at crossed and leftward at 501uncrossed disparities fall in the 'SD' condition. 502

The results supported both of our predictions. We found 503 increased disparity dependency in motion adaptation 504

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Figure 5. Results from motion adaptation to double opposing surfaces. The figure format and symbols are same as in Figures 2A, 2C, and 2E. A–B: Plots of 75% detection thresholds for the testers with the adapted disparity (A) and with the different disparity (B). C: Al's for motion detection with double surfaces.

505 compared to that in the single surface experiment. We 506 plotted thresholds from post-adaptation against those from 507 pre-adaptation (Figures 5A and 5B) and AIs from 'SD' 508 condition against those from 'SS' (Figure 5C). The 509 increase in detection thresholds after adaptation was significant (p < .01 for Wilcoxon's matched pairs test) 510for 'SS' condition but not (p = .63) for 'SD' condition. 511Accordingly, AIs were significantly larger than zero in 512the 'SS' condition (mean AI = .07, p < .01) but not in 513'SD' condition (mean AI = .01, p = .4). Wilcoxon's 514matched pairs test showed the AIs from the 'SS' and 'SD' 515conditions were significantly different (p < .05). For direct 516comparison between CIs of the single- and double-surface 517experiments, examine Figures 6E to 6A. The average CI 518substantially shifted in positive direction in the double 519surface experiment (1.1, the arrow in Figure 6E; The 520average CI was significantly larger than zero. p < .05 for 521Wilcoxon signed rank test), as compared to the single 522surface experiment (.32, the arrow in Figure 6A; The 523average CI was not significantly different from zero. p = .49524for Wilcoxon signed rank test). Also, the number of AI 525pairs that showed significant differences between the 'SS' 526and 'SD' conditions increased to 7 with double surfaces 527(red triangles in Figure 6E), from zero with a single 528surface (no colored triangles in Figure 6A). Lastly, the 529linear relationship between the size of pooled AI and the 530magnitude of CI, which was the characteristic feature 531of contingent adaptation in stereo detection, was evident 532(r = .5, p < .05) in the double surface experiment but not 533in the single surface experiment. 534

In order to examine our second prediction on the overall 535magnitude of adaptation, we compared the magnitudes of 536AIs from the 'SS' condition between the double- and 537 single-surface experiments. Among the 19 AIs in the 538single surface experiment, except two data points from the 539observer (SK) who participated only in the single-surface 540experiment, 17 AIs had matched adaptor types and con-541trast levels in double-surface experiment. As predicted, 542the average AI for the 'SS' condition in double-surface 543experiments (.08) was smaller than that in single-surface 544experiments (.14), although the difference between the 545average AIs turned out to be marginally insignificant 546(Wilcoxon's matched pairs test, p = .055) based on a small 547 sample size of 17. The within-adaptor comparison 548between single- vs. double-surface adaptors is shown in 549Supplementary Figure 2. In about half pairs (8 out of 17), 550AI from the single-surface experiment was significantly 551larger than that from the double-surface experiment with 55295% confidence intervals under the bootstrap-generated 553distribution. In summary, we conclude that the adaptor of 554double opposing surfaces increased disparity contingency 555of direction-selective adaptation but decreased the overall 556magnitude of motion adaptation. $557 \\ 558$

Discussion

The most prominent finding in our study is the asymmetrical interaction between motion and stereopsis in 563 adaptation. Concurrent adaptation impaired the performance 564



Figure 6. Contingency between motion and stereo adaptation. In each panel, contingency indices are plotted against pooled AIs and summarized in histograms on top. A pooled AI is an overall magnitude of adaptation in a given condition and was obtained by taking the squared root of the sum of the squared AIs from the condition where the task-irrelevant feature was the same as the adaptor and that where it was different. The colored symbols both in plots and histograms are AI pairs that showed significant difference with the 95% confidence interval under bootstrap-generated data sets; red for larger AI from the condition where the task-irrelevant feature differed from the adaptor. The correlation coefficient between the pooled AI and CI with its significance (*, p < .05 and **, p < .01) is shown in each panel. The arrow in each histogram is the average CI. A–B. Motion adaptation. C–D. Stereo adaptation. E. Motion adaptation with double surface adaptor.

565of detecting disparity-defined coherent surface when tester dots were moving in a direction identical to the adaptor, but 566enhanced the performance when the tester was moving in 567 568the opposite direction. Such strong contingency of disparity adaptation on direction was in sharp contrast with little 569contingency of motion adaptation on disparity. This 570asymmetry in direction and disparity adaptation is not 571likely to be due to the lack of disparity adaptation. First, the 572disparity range we used in the current study was carefully 573574selected based on the known disparity selectivity in humans. Although the width of disparity tuning in some 575neurons of monkey MT is as large as 1 deg (DeAngelis & 576Newsome, 1999), humans are able to detect much finer 577 disparities down to 2 arc min (Blackmore & Julesz, 1971; 578Stevenson, Cormack, Schor, & Tyler, 1992) but often lose 579good perception of depth when the disparity is larger than 5801° (Backus, Fleet, Parker, & Heeger, 2001). The disparity 581range used in the current study is considered as optimal 582for human perception of disparity-defined surfaces and has 583been reported to generate substantial adaptation effects 584(Stevenson et al., 1992). Nevertheless, we performed a set 585of control experiment using adaptors without coherent 586 motion and successfully demonstrated a substantial 587 amount of disparity-selective adaptation in our stimuli. 588

The strong asymmetry between motion and stereopsis in 589adaptation has not been previously reported and may be 590considered as a conflict to the previous reports of disparity-591selective directional aftereffects (Anstis & Harris, 1974; 592Verstraten et al., 1994; Sohn & Seiffert, 2006). We showed 593that this discrepancy was due to the use of different 594adapting stimuli. By pitting against two antagonistic values 595in each feature domain during adaptation, previous studies 596had effectively demonstrated the existence of joint pro-597 cessing of two features, but cannot provide a fair quan-598titative description of mutual influences between motion 599600 and stereopsis.

Motion precedence over disparityin processing dynamic 3-D surfaces

In observers' task in our study, where they had to detect a 603 surface of coherent dots embedded in noise dots, direction 604 605 or disparity signals must be pooled over a large space. One 606 possible interpretation of the asymmetry in contingency is that the neural mechanism underlying the integration of 607 local motion signals precedes that underlying the integra-608 tion of local disparity signals somewhere along the 609 hierarchy in the construction of global surfaces. 610

Motion precedence over disparity in global integration is not surprising given what we know of how the visual system encodes the two features. Direction selectivity is found as early as at the level of retina in rabbits (Barlow, Hill, & Levick, 1964; Taylor, He, Levick, & Vaney, 2008), and in primate V1, motion is processed by the monocular as well as binocular neurons (Hubel & Wiesel,

1968). On the other hand, information of binocular 618 disparity is not available before V1, where signals from 619 the two eyes are first combined. In addition, it is known 620 that the basic characteristics of direction-selectivity in V1 621 are well preserved in a subpopulation of MT neurons that 622 receive projections from V1 (Movshon & Newsome, 623 1996) whereas disparity-selectivity in the primary visual 624 area and that observed in extrastriate areas exhibit quali-625 tative differences (Cumming & DeAngelis, 2001). A recent 626 study on monkeys (Ponce, Lomber, & Born, 2008) sug-627 gests that direction selectivity of neurons in MT is depen-628 dent largely on direct input from V1 whereas disparity 629 selectivity in MT requires an involvement of V2/V3 at 630 intermediate processing stages. The authors inspected 631 changes in direction and disparity tuning of MT neurons 632 while inactivating indirect pathways (V2 and V3) from V1 633 to MT. The directional tuning curves of MT neurons were 634 well preserved whereas their disparity tuning curves were 635 substantially distorted during inactivation of V2 and V3. 636 In line with these reports, our findings suggest that the 637 processing of motion information is completed earlier and 638 affects the process of encoding disparity information. 639

We are not arguing here that motion integration occurs 640 entirely independent of disparity information. For example, 641 local cancellation between directionally opposed motion 642 signals paired within a small region is dependent upon 643 whether or not opposed motion signals are presented at 644 the same disparity (Qian, Andersen, & Adelson, 1994). 645 This implies that the fine-spatial-scale interaction between 646 motion signals is affected by joint relationship between 647 disparity and direction. We underscore that the perceptual 648 task in our study taps the process of constructing coherent 649 global surfaces out of local signals, rather than the encoding 650of local motion and disparity signals. Only globally 651coherent directional signals, but not local random motion, 652 affected detection performance of disparity-defined sur-653 faces after adaptation (stereo adaptation experiment without 654 coherent motion). Such dominance of motion over disparity 655 in perception of global surfaces in our study is also con-656 sistent with previous studies using non-adaptation para-657 digms (Hibbard, Bradshaw, & DeBruyn, 1999; Lankheet & 658 Palmen, 1998; Muller, Lankheet, & van de Grind, 2004) 659 that reported strong motion dominance over disparity 660 information in spatial integration tasks. 661 662

Potential neural substrates for the asymmetry 663

In the cortical pathways processing motion and stereopsis, 664 we conjecture MT as the most probable neural locus respon-665 sible for the observed asymmetry in contingency. Neurons 666 in MT are known to integrate local inputs over a larger 667 region of visual space than do their cortical afferents (Croner 668 & Albright, 1999), which has been reported both for motion 669 (Movshon & Newsome, 1996) and disparity (DeAngelis & 670 Uka, 2003). Our finding that disparity-selective adaptation 671



Figure 7. Hypothetical and observed contingency tables of adaptation effects. The four cells in each 2×2 contingency table represent categorical test conditions, which are the combinations out of adapted and non-adapted directions (columns) and disparities (rows). The adaptor corresponds to the top left cell (adapted in both direction and disparity). Color describes adaptation effects normalized within each unit (A) or experimental condition (B). Hue indicates the sign of adaptation, red for conventional adaptation and blue for null adaptation. Brightness indicates the magnitude of adaptation, 0 for no adaptation and 1 for the largest adaptation effect in a given unit of neural population (A) or experimental condition (B). A. Hypothetical adaptation effects that will be observed in three different neural populations; nonjoint direction-selective unit, nonjoint disparity-selective unit, and jointly selective unit, from left to right. B. The observed adaptation effects from the motion detection experiment (left) and from the disparity detection experiment (right). The number in each cell is the Al averaged across data from all of the observers (arrows in Figures 2E, 2F, 3E, and 3F). For visual comparison with the hypothetical adaptation effects in A, we computed the normalized Als, which are indicated by color, by dividing the averaged Als by the largest average Al in a given contingency table.

was contingent upon co-located global coherent motion,
but not upon local random motion, supports the idea that
MT plays a major role in the extraction of feature-defined
surfaces in the current study.

Our concurrent adaptation paradigm was designed to 676 measure the extent to which three potential neural popu-677 lations contribute to the encoding of surfaces defined jointly 678 by direction and disparity: nonjoint direction-selective, non-679 joint disparity-selective, and joint selective units (Figure 7A, 680 from left to right). Our results from single-surface adaptor 681 682 experiment (Figure 7B) are qualitatively close to the pattern of adaptation predicted by the nonjoint direction-683 selective units (the leftmost panel in Figure 7A). This 684 motion dominance in concurrent adaptation may be 685 explained by the imbalance between the three groups of 686 neural population in MT. In MT, nearly all neurons are 687 direction-selective (Albright, 1984; Maunsell & van 688 Essen, 1983a; Snowden, Treue, & Andersen, 1992; Zeki, 689 690 1974) whereas only 60 (Maunsell & van Essen, 1983b)-691 90% (DeAngelis & Uka, 2003; Palanca & DeAngelis, 2003) of neurons are tuned for disparity. Also, the degree
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of selectivity is greater for direction than for disparity. In
addition, MT clearly has a subregion of direction-selective
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cells with poor disparity tuning and a subregion of jointly
selective cells, but little of disparity-selective cells with
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poor direction selectivity (DeAngelis & Newsome, 1999).
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This disproportion in functional architecture of MT is 698 consistent with our findings in many aspects. First, it 699 explains the asymmetry in contingency in the single-700 surface adaptation. Since a single surface adapts both non-701 joint direction-selective units and jointly selective units in 702 MT, motion detection, which can be performed based on 703 contributions from either units, is not dependent much on 704the disparity of stimuli ('motion detection' in Figure 7B). 705In contrast, because disparity detection requires contribu-706 tions mostly from the jointly selective units, it would be 707 highly dependent on the direction of stimuli ('stereo 708 detection' in Figure 7B). Next, double opposing surfaces 709 would adapt only jointly selective units in MT because 710 non-joint direction-selective units do not respond to 711

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opposing directions of motion due to mutual suppression (Bradely, Qian, & Andersen, 1995). Under this condition, motion detection as well as disparity detection is highly contingent upon each other because performing the motion task is now determined by the contribution from the jointly selective units. Lastly, the single-surface stimulus adapts both non-joint direction-selective units and jointly selective units whereas the double surfaces adapt only jointly selective units, resulting in the total

721 amount of direction-selective adaptation being greater for 722 the former. In our double-surface experiment, the average 723 direction-selective AI for the adapted direction and 724 disparity was only 61% of direction-selective AI with 725 the single-surface adaptor, which is comparable to the 726 reported 68% of disparity-selective neurons in MT from 727 an early study (Maunsell & van Essen, 1983b).

While the above explanation based on the imbalance 728 between heterogeneous MT populations can serve as an 729 underlying mechanism for the observed asymmetry, there 730 may be another explanation. Different tuning properties of 731MT neurons for direction and disparity may also explain 732the observed asymmetry. In our study, disparity selective 733 adaptation was probed by the two disparity levels that are 734only apart by 0.4 deg whereas direction selective 735 adaptation by opposite directions. The two test directions 736 737 in the current study may be different enough to activate separate populations of MT neurons due to relatively 738 narrow direction tuning curves, but the disparity differ-739 ence in the current study be rather narrower than that can 740 be distinctively represented by some of MT neurons, 741whose disparity tuning width can be as large as 1 deg 742 (DeAngelis & Newsome, 1999). Even though we dem-743onstrated that the amount of perceptually measured 744 disparity-selective adaptation was significant and compa-745 rable to that of direction-selective adaptation, the near and 746 747 far disparity in the present study may have adapted a subpopulation of MT neurons with similar strength given 748 the disparity tuning width of MT neurons. This wide tuning 749property for disparity may have contributed to the weak 750disparity contingency in direction selective adaptation that 751we observed. The explanation based on different tuning 752753properties for direction and disparity is not contradictory nor mutually exclusive with the imbalance hypothesis 754suggested above. Instead, they may well exist in parallel 755and contribute to the asymmetric interaction between the 756 two features. 757

760 Concluding remarks

The concurrent adaptation paradigm enabled us to quantitatively assess the relative influence of two features and infer the processing precedence, which have not been addressed by previous studies. Our proposed explanation of the asymmetric contingency effects based on the disproportion of joint and non-joint feature-selective neural 767 populations is applicable to previously reported contingent 768 aftereffects in other feature domains, where two opposing 769values in each feature were employed as an adaptor: orien-770tation and color (McCollough, 1965); color and motion 771 (Favreau, Emerson, & Corballis, 1972). Our findings warn 772 us to exercise cautions when interpreting contingent after-773 effects as evidence for neural mechanisms for reciprocal 774processing between two features. Our concurrent adapta-775tion procedure and analysis offer a valid and effective 776 means of studying interactions between multiple features. 777 Furthermore, the experimental results may provide a 778 prediction for neural substrates underlying adaptive changes 779 in perception of stimuli defined by multiple features in any 780 future electrophysiological or imaging studies. 781

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