Physics embedded in visual perception of three-dimensional shape from motion

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Visual perception, and by implication underlying neural events, can become unstable when optical information specifying objects is ambiguous. Here we report that one striking form of instability—perceived three-dimensional structure-from-motion (SFM)—can be stabilized when an otherwise ambiguous object appears within a context implying frictional interactions with another rotating object; violations of physical conditions specifying friction disrupt stabilization. Evidently, information about frictional interaction is embedded within neural mechanisms specifying SFM.

Perception of a rotating three-dimensional (3D) object can be generated from motion of its two-dimensional projected features[1,2], the phenomenon called SFM. Without explicit depth cues, however, the surface ordering and direction of rotation are completely ambiguous, causing people to experience alternative perceptual interpretations over time[3]. When a real, rotating sphere contacts another, stationary sphere, the transfer of rotational kinetic energy arising from friction causes the previously stationary sphere to rotate. For a pair of contiguous spheres that rotate about parallel axes, friction dictates opposite directions of rotation. Is frictional interaction also embodied in perceptual mechanisms that register SFM?

To find out, we measured rotational coupling between a pair of computer-generated SFM spheres defined by dots scattered over their surfaces (**Fig. 1a**); one sphere's direction of rotation was ambiguous but the other's was unambiguously clockwise (CW) or counter-clockwise (CCW) owing to occlusion of dots on the back of the sphere and smooth variation of the luminance of dots on the front of the sphere (see **Supplementary Methods** online). Using key presses, observers indicated when the spheres appeared to rotate "in the same direction" (co-rotation) or "in opposite directions" (counter-rotation). When the two spheres appeared to touch, observers overwhelmingly perceived counter-rotation ($t_4 = 8.2$, $P < 0.01$), but when a very small gap separated the spheres the incidence of counter-rotation dropped sharply and, for some observers, gave way to co-rotation[4,5] (**Fig. 1b**). This effect also occurs for pairs of cylinders or for a cylinder and sphere in frictional contact. Strong counter-rotation also was observed when a thin, opaque rectangle (the same size as the gap used above) was presented stereoscopically in crossed disparity, thereby occluding the region of contact between the two spheres ($t_3 = 5.5$, $P < 0.025$). Thus, frictional interaction does not require explicit encoding of local motions where the spheres touch (**Fig. 1b**). We also replicated experiment 1 with a pair of spheres rotating about their horizontal axes (so that the local motions for all dots were vertical). Consistent with friction, co-rotation was predominantly seen when the spheres appeared to touch ($t_3 = 5.92$, $P < 0.01$) but not when they were separated by a small gap (**Fig. 1c**).

Manipulations of angular velocity that violate implied friction disrupt the incidence of counter-rotation (**Fig. 2a**). Observers tracked rotational coupling between an ambiguous sphere and an unambiguous sphere rotating at the same angular velocity (both 10 rpm or both 20 rpm) or at different angular velocities (one 10 rpm and one 20 rpm). Perception of counter-rotation was robust when velocities matched ($t_3 = 4.2$, $P < 0.025$), but not when velocities were mismatched.

Considered together, these results argue against local motion interactions, such as motion priming or center/surround motion opponency, as the basis of rotational coupling[6], instead implicating friction as the causal agent. But are observers merely reporting what they believe should happen? To address this possibility, we exploited a well-established adaptation phenomenon whereby exposure to an SFM sphere rotating unambiguously in a given direction subsequently causes an ambiguous SFM object to appear to rotate in the opposite direction for a short time[7]. Observers adapted for 60 s to

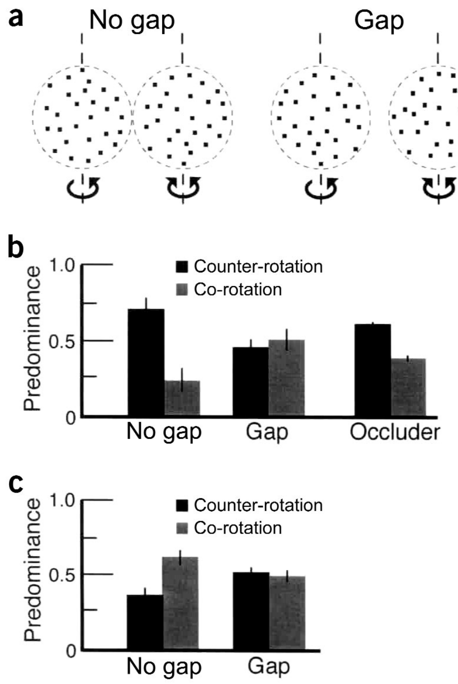

Figure 1 Effect of frictional interactions on perception of 3D-SFM. (**a**) Schematic of stimuli and configurations used in experiment 1. Spatial separation between spheres was either 0 (no gap) or 6.33′ (gap). Spheres were created by the lateral motions of hundreds of white dots scattered over the surface of two virtual globes each 1.06° in diameter (see **Supplementary Methods**). (**b**) Results of experiment 1. Average predominance (percent total viewing duration) of counter-rotation (black bars) and co-rotation (gray bars) as a function of spatial separation ($n = 5$). Data were collapsed across rotation direction and spatial configuration, as there were no systematic differences for these factors; these predominance values may not sum to unity owing to brief transition periods when neither key was pressed. Counter-rotation was perceived more often than co-rotation when the region of contact between a pair of contiguous spheres was occluded by a thin vertical rectangle ($n = 4$). (**c**) Average predominance of counter-rotation and co-rotation as a function of spatial separation for a pair of spheres rotating about their horizontal axes ($n = 4$). Error bars in **b** and **c** are ± 1 s.e.m.

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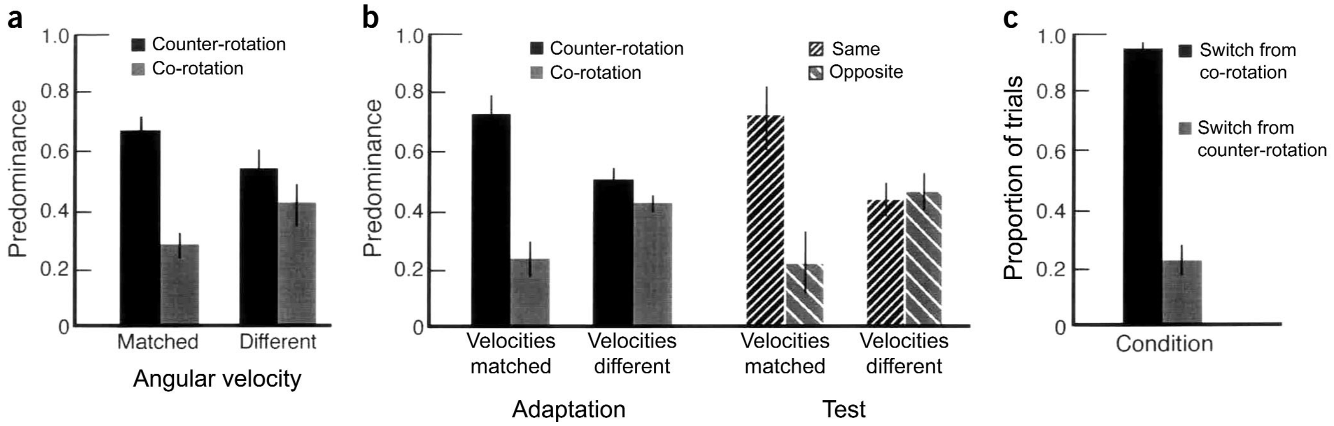

Figure 2 Results of experiments 2–4. Data are collapsed across rotation direction and spatial configuration; error bars are ± 1 s.e.m. (**a**) Experiment 2. Counter-rotation (black bars) was perceived more often than co-rotation (gray bars) when the angular velocities of the ambiguous and unambiguous spheres were matched ($n = 4$). (**b**) Experiment 3. Left: during adaptation, counter-rotation was predominantly perceived when the angular velocities of the spheres were matched, but not when they were mismatched. Right: during postadaptation test, a single, ambiguous SFM sphere predominantly rotated in the direction opposite that experienced while viewing the ambiguous globe during adaptation, but only when the velocities of the unambiguous and ambiguous spheres matched during adaptation ($n = 4$). (**c**) Experiment 4. Proportion of trials on which a physical reversal in rotation direction of the unambiguous sphere triggered a switch from one type of rotational coupling to the other ($n = 5$). Switches from co-rotation to counter-rotation (black bars) occurred more frequently than switches from counter-rotation to co-rotation (gray bars).

displays in which a pair of contiguous spheres rotated either at the same velocity or at different angular velocities. Immediately thereafter, they tracked for 15 s the rotation of a single ambiguous SFM sphere presented at the same spatial location as the ambiguous 'adaptation' sphere. When the angular velocities of the two spheres were matched, thereby implying frictional interaction, the ambiguous SFM sphere was effectively stabilized during the adaptation period ($t_3 = 4.3$, $P < 0.025$); when the velocities were mismatched during adaptation, the ambiguous sphere alternated irregularly between CW and CCW. Notably, during the test period observers predominantly perceived rotation opposite to that reported during adaptation ($t_3 = 4.2$, $P < 0.025$), but only when the spheres' velocities were matched (**Fig. 2b**). The strong aftereffect produced by exposure to frictional counter-rotation implies that this contextual effect is genuinely grounded in visual processing.

In bistable dynamical systems, the likelihood of transitions between states depends on the relative strengths of those states[8]. To learn whether this applies to frictional interactions, we instigated a reversal in the direction of rotation of the unambiguous sphere while observers were perceiving either co-rotation (a relatively weak state) or counter-rotation (a relatively strong state). Note that after this physical reversal, the persistence of either type of rotational coupling requires a concomitant perceptual reversal of the ambiguous sphere. We found that switches from counter-rotation to co-rotation were indeed much less likely than switches from co-rotation to counter-rotation (**Fig. 2c**). Thus, perturbations that would otherwise result in a switch from a more stable state (counter-rotation) to a less stable state (co-rotation) are resisted, even though this requires perceptual reorganization of the ambiguous sphere. This finding further demonstrates the enhanced stability of counter-rotation in contexts implying friction.

Evidently, then, specification of 3D objects defined kinetically can be influenced by natural mechanical forces. Current accounts of SFM implicate cortical area MT as an important component in the neural substrate mediating perception of 3D-SFM[9–12], so it would be informative to determine whether implied friction modulates MT neural activity using ambiguous SFM. Friction's contextual effect also needs to be incorporated into computational models of SFM in which bistability is generated by the interplay among recurrent excitatory and inhibitory signals[13]. Small shifts in the balance of activity within this kind of network produce pronounced changes in dynamics, and friction's contextual effect could be instantiated by intrinsic connections or through feedback. However accomplished, implied frictional interactions underscore that visual perception is a dynamic, constructive process employing heuristics acquired through evolution and during the lifetime of an organism[14,15].

Note: Supplementary information is available on the Nature Neuroscience website.

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COMPETING INTERESTS STATEMENT
The authors declare that they have no competing financial interests.

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