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Vision Research 46 (2006) 4007–4023
Vision Research
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Subjective appearance of ambiguous structure-from-motion can be driven by objective switches of a separate less ambiguous context

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Received 23 September 2005; received in revised form 4 July 2006

Abstract

Two ambiguous transparent structure-from-motion (SFM) stimuli often appear to co-rotate. Grossmann & Dobbins (2003) reported breakdown of such perceptual coupling when one stimulus was made unambiguous (by rendering it opaque), leading them to propose that coupling depends generally on differential stimulus ambiguity. In contrast, we demonstrate robust stimulus-driven coupling even when one SFM stimulus is relatively disambiguated, by using relative-luminance and/or binocular-disparity cues. Such context stimuli could induce stimulus-driven coupling by disambiguating the transparent stimulus, though critically only when the context was clearly non-opaque and coaxial with the ambiguous stimulus. This demonstrates long-range information-sharing between separate stimulus representations, subject to specific constraints.

Keywords: Structure-from-motion; Kinetic depth effect; Contextual integration; Ambiguity; Multistability; Human vision; Perceptual grouping

1. Introduction

In contemporary examples of the kinetic depth effect or KDE (Miles, 1931; Wallach & O'Connell, 1953), also known as structure-from-motion (SFM, e.g., Andersen & Bradley, 1998; Nawrot & Blake, 1989; Ramachandran, Cobb, & Rogers-Ramachandran, 1988; Treue, Husain, & Andersen, 1991), two overlapping opposite-motion random-dot fields may create the appearance of a transparent object with curved surfaces rotating in depth (e.g., a virtual cylinder, see Fig. 1). Such random-dot kinematograms (RDK) can be spontaneously 'bistable', subjectively switching direction of apparent rotation back-and-forth unpredictably, even though the actual display-sequence remains physically unchanged. Moreover, an interesting perceptual-coupling phenomenon can be observed when a display contains multiple ambiguous stimuli of this type (e.g., Bonneh & Gepshtein, 2001; Eby, Loomis, & Solomon, 1989; Gillam, 1972). While the timing of perceptual reversals remains stochastic, some or all stimuli in the display may now appear phenomenally to switch direction together. Such 'spontaneous coupling' has been found for a wide variety of ambiguous stimuli that can lead to bistable percepts, including Necker cubes, triangles, rotating contours or planes, and dynamic dot-quartets (e.g., Adams & Haire, 1958; Attneave, 1968; Ramachandran & Anstis, 1983).

One attractive interpretation of such spontaneous-coupling phenomena is that they may reflect sharing of information between representations of the different stimuli, so that perception of each local stimulus converges on a unified interpretation of the global scene (e.g., Attneave, 1968; Ramachandran & Anstis, 1983). If such an 'information-sharing' account were shown to apply, then such coupling phenomena would become pertinent to investigations of how our visual system integrates information from surrounding context to make sense of local ambiguities. Such information-sharing would predict not only that perceptions of *ambiguous* stimuli can become coupled together, as described above but also that interpretation of an ambiguous stimulus could become determined by (and thus

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doi:10.1016/j.visres.2006.07.008

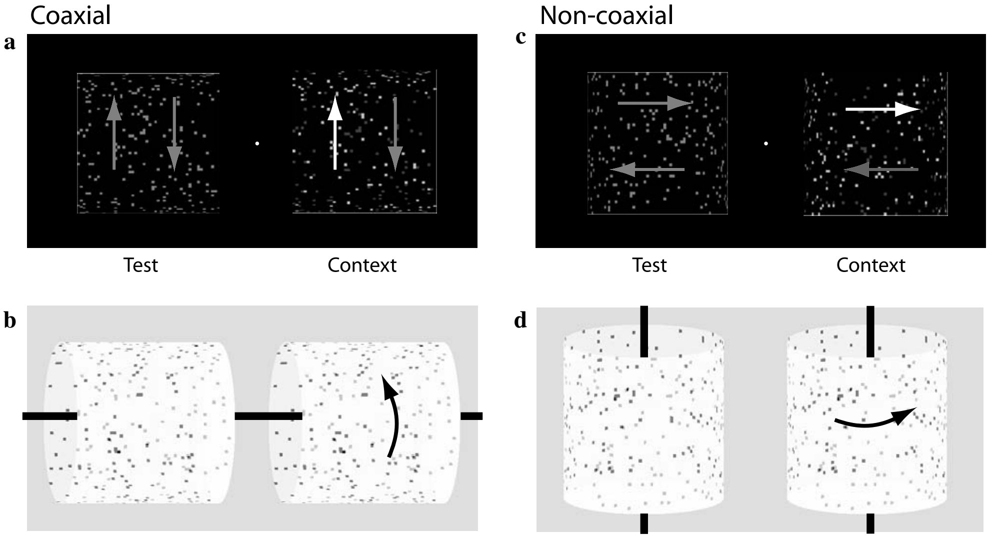


Fig. 1. Examples of random-dot kinematogram stimuli used in Experiment 1. (a) Approximate stimulus appearance on screen for cylinders with horizontal rotational axes in coaxial formation; arrows added to indicate direction of dot motions for this example. The transparent 'Test' stimulus is displayed on the left, with all dots having the same luminance (i.e., inter-dot contrast = 0%); a translucent 'Context' stimulus is displayed on the right with different luminances for dots moving in opposite directions (e.g., inter-dot contrast = 50%). The brighter dots are here shown moving upward, thus biasing perception towards upward rotation of the 'front' surface. (b) 3D-rendered schematic of coaxial cylinders, with the 'Context' biased by the inter-dot contrast towards upward rotation. Under stimulus-driven coupling, the Test stimulus should appear to rotate in the same direction as the Context (see main text). (c and d) Non-coaxial stimuli and 3D renderings.

coupled with) appropriate *un*ambiguous (or less ambiguous) context stimuli (Eby et al., 1989; Gillam, 1976; Grossmann & Dobbins, 2003).

Despite the intuitive plausibility of such information-sharing, direct support from cases of apparent motion, KDE or SFM has remained surprisingly elusive. For example, unambiguous apparent motion reportedly had little effect on interpretation of ambiguous quartet-motion (Ramachandran & Anstis, 1983), even though spontaneous coupling is very striking when all the quartet stimuli are ambiguous. The main evidence reported to date of unambiguous KDE or SFM context stimuli having an influence on ambiguous perception was for exceptional situations where stimuli were concentric or touching (e.g., Eby et al., 1989; Fang & He, 2004; Gilroy & Blake, 2004). Coupling was sharply reduced even for small inter-stimulus separations (Gilroy & Blake, 2004). While such very short-range contextual disambiguation effects may be compelling when found, their relevance to longer-range disambiguation (comparable to the long-range spontaneous coupling that can be readily observed between concurrent bistable stimuli) remains unclear.

One particularly intriguing set of results was recently reported by Grossmann & Dobbins (2003), who set out to examine whether contextual stimuli can influence separate concurrently presented, ambiguous SFM objects. However their results seem to argue *against* an information-sharing account of coupling (at least of the kind stated above for long-range interactions). They presented two stimuli (e.g., random dots kinematograms or wireframe structures) up to 10° apart, which could each be perceived as 3D objects rotating in depth. When both were perfectly transparent, such that the direction of rotation was ambiguous for both, strong spontaneous coupling was found between them (in line with the above-cited examples of spontaneous coupling). Both tended to be perceived as rotating subjectively in the same direction, switching spontaneously together. Surprisingly, however, when the rotation of one stimulus was physically disambiguated by rendering it *opaque* (i.e., with only one direction of dot-motion now visible, thus making its direction of rotation highly *un*ambiguous), such coupling between the local percepts was dramatically decreased, apparently contrary to what might be expected from information-sharing.

To account for their observed reduction in subjective coupling with less ambiguous contexts, Grossmann & Dobbins (2003) proposed a hypothetical mechanism whereby feedback from higher to lower visual areas may function to select and stabilise stimulus interpretations. They argued that the influence of such feedback would be global, affecting multiple ambiguous stimuli in the same way across the visual field, thus accounting for the subjective coupling commonly observed between these. They further proposed that such feedback influences may be strongest for ambiguous stimuli (given their arguably greater need for selection and stabilisation), while unambiguous stimuli should involve the least feedback. Taken together, the various premises in this 'ambiguity-dependent-feedback' account could explain the breakdowns in coupling with an unambiguous (e.g., opaque) context, as observed by Grossmann & Dobbins. However if applied more generally, this account seems to imply that an ambiguous stimulus should not be influenced by its context unless that context is itself also relatively ambiguous. This appears to run counter to the intuitive idea that information-sharing may lead to maximal disambiguation from relatively unambiguous contexts.

Proponents of information-sharing (e.g., Attneave, 1968) might argue that the various phenomena of spontaneous coupling (Eby et al., 1989; Gillam, 1976; Grossmann & Dobbins, 2003) still provide direct evidence of active information sharing, at least between multiple *ambiguous* stimuli. However, it may in fact be possible (in principle at least) to explain even that basic observation, without invoking any information-sharing processes whatsoever. Moreover, such an alternative account might also explain the lack of coupling with an unambiguous stimulus that Grossmann & Dobbins (2003) observed, and also why past demonstrations of contextual disambiguation may have been so sparse.

Such an account would simply propose that spontaneous coupling between multiple ambiguous stimuli might just reflect some common *internal noise* source, that globally affects stimuli across the visual field. For example, some perceptual switches might conceivably be caused by blinks, involuntary fluctuations of attention, small eye-movements, or other stochastic sources of internal 'noise'. Any such internal events might, in principle, simultaneously perturb the finely balanced perceptual states of similar ambiguous stimuli across the whole visual field. Note that such accounts need not assume any active *sharing* of information between representations of the different ambiguous stimuli. Instead, each bistable stimulus might in principle be separately influenced by the same stochastic global variable (e.g., random perturbation of generic internal noise), rather than stimulus representations influencing each other directly via information-sharing.

For the particular case of Grossmann & Dobbins' (2003) observed reduction of subjective perceptual coupling with a less ambiguous (opaque) context, one might then argue that an *un*ambiguous (or less ambiguous) stimulus will simply be more resistant to any perturbations in internal noise than for an ambiguous stimulus, because it provides a stronger signal. Thus, while the fine balance between alternative perceptual states for an ambiguous stimulus might be readily tipped either way by spontaneous fluctuations of stochastic internal noise, the perception of a neighbouring disambiguated stimulus should remain relatively immune to such noise, hence resulting in little or no apparent perceptual coupling between such different stimulus types.

Thus, much of the past evidence for spontaneous coupling could (in principle at least) be explained away as potentially reflecting stochastic internal noise, without necessarily implicating true sharing of information between stimulus representations. This possibility arises in part due to the common use of paradigms in which 'spontaneous' perceptual changes must (by definition) reflect unobservable internal factors. In a typical paradigm of this type, the observer watches the same stimulus (e.g., a repeating animation loop) for an extended period, indicating when their subjective perception switches. As there is no external stimulus change in such a situation, a perceptual change can only reflect some stochastic internal process.

Here, we used a different approach that, by design, relied instead on *objective* external events to trigger a subjective perceptual switch. We periodically introduced veridical rotation-reversals into a separate *context* stimulus, while measuring the extent to which those external stimulus-driven signals could drive reversals of a bi-stable percept for a concurrent ambiguous *test* stimulus. Measuring any correspondence between the veridical context-state, and the subjective state for the ambiguous test stimulus, yields a measure of *stimulus-driven coupling*. We aimed to use this new measure of stimulus-driven coupling to discriminate between the three different accounts of coupling introduced above: namely, the internal-noise account; Grossmann & Dobbins' (2003) ambiguity-dependent-feedback account; or coupling based on information-sharing.

As will be seen, our new results go against Grossmann & Dobbins' (2003) proposal of a general rule that relatively unambiguous stimuli cannot induce coupling. Instead, we find that contexts that are effectively disambiguated (i.e., containing a substantial stimulus bias that invariably biases subjects' reported perceptions in favour of one particular direction of rotation) can in fact induce robust (stimulus-driven) coupling with percepts for an ambiguous SFM stimulus, provided certain conditions are met. From this new perspective, Grossmann and Dobbins' own results then appear more as interesting exceptions to information-sharing, rather than as illustrations of a general rule that such sharing can never arise between ambiguous and less ambiguous stimuli.

Specifically, in Experiment 1, we found that relatively disambiguated (stimulus-biased) contexts can in fact drive strong coupling, but subject to two critical constraints. First, stimulus-driven coupling was found only when the front and back surfaces of the inducing context SFM stimulus were both clearly visible (i.e., as for clearly translucent but not for opaque contexts, nor for those approaching opacity); secondly only when the rotating translucent context and the test stimuli were arranged into a coaxial configuration. Experiment 2 controlled for low-level differences between translucent and opaque stimuli, but found that visibility of both front and back-surfaces (clear translucence) in the context was still a critical factor for stimulus-driven coupling. Experiment 3 explored the configural constraints on such stimulus-driven coupling further, indicating that this may be stronger when context-test pairs appear to rotate in 3D around a common axis. Finally, Experiment 4 sought to disambiguate the translucent context even further by adding stereo-disparity cues to luminance cues, thus providing additional redundant cues indicating which moving 'surface' was in front and which behind. Such 3D contexts were always perceived veridically, with no inappropriate perceptual reversals even for very extended viewing epochs. Yet, these highly unambiguous stimuli still-induced strong stimulus-driven coupling with perception of the ambiguous test. These experiments all confirm that a highly disambiguated context can induce coupling, but subject to specific constraints.

Although our experiments follow on from Grossmann and Dobbins' pioneering (2003) work, in the topics addressed, in fact our studies were first instigated independently of that work, and so differ in several respects. Grossmann and Dobbins typically measured spontaneous coupling between *subjective* percepts for the context and test stimulus, while here we focus on stimulus-driven coupling of test percepts with the *objective* context state. This measure yields a pattern of results that cannot be inferred from the original measure of spontaneous coupling alone. For instance, our Experiment 1 revealed that stimulus-driven coupling does not monotonically decline with decreasing context ambiguity (i.e., with increased opacity), unlike the more traditional measure of purely subjective spontaneous coupling, which did follow a monotonically decreasing function here, akin to that found by Grossmann & Dobbins (2003, see section 8 of their paper). A further difference in the present experiments was that we combined manipulations of context translucency together with veridical switches in context rotation-direction, within the same individual experiments (rather than separately, as in Grossmann and Dobbins, c.f. sections 5 versus 8 of their paper), thus enabling us to make the critical observation of stimulus-driven coupling with translucent context stimuli. Finally, we also examined the impact of configuration and axial alignment between context and test stimuli here, while Grossmann and Dobbins only used coaxial stimuli.

Some of our results do replicate and corroborate aspects of Grossmann & Dobbins' (2003) findings, particularly as regards the ineffectiveness of opaque contexts in inducing coupling. However, our new data provide decisive evidence that, under appropriate conditions, effectively disambiguated contexts (see Experiment 4 in particular) can induce strong coupling, while the ambiguity-dependent-feedback model would predict only weak or no coupling. These observations thus lead us towards very different theoretical conclusions, which favour information-sharing between stimulus representations, subject to specific constraints.

2. General methods

2.1. Subjects

A total of 20 naïve observers aged between 20 and 30 participated in at least one experiment, for monetary reward. There were 7 observers in Experiment 1, and 8 in Experiment 2 (of whom 5 had performed in the first). A new set of 7 observers participated in Experiment 3, and the final Experiment 4 had 5 observers (3 new). All had normal or corrected vision by self-report.

2.2. Stimuli and apparatus

Stimuli were presented on a 19" CRT display (Sony 500PS CRT monitor in Experiments 1 and 2; Mitsubishi Diamond Pro in Experiments 3 and 4), viewed from a distance of 1 m in a darkened room. Video mode was 1600 × 1200 pixels, with a screen refresh rate of 60 Hz. Displays were linearized using 8-bit software gamma-transformation to produce a mid-gray background luminance of 40 $\mathrm{cd\,m^{-2}}$. Stimulus control was provided by a PC running Matlab and Psychophysics Toolbox (Brainard, 1997). Responses were made using the standard PC keyboard. In Experiment 4 only, stereo depth cues were displayed using Stereographics CrystalEyes LCD shutter-glasses to present stimuli with opposite binocular disparities to left and right eyes alternately (at 30 Hz synchronised with the screen refresh).

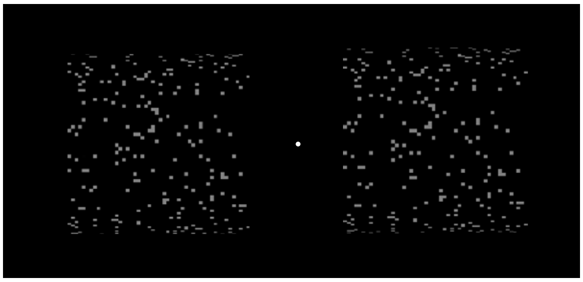
In all experiments, the main stimuli were random-dot kinematograms (RDK) composed of two superimposed fields of randomly distributed small square 'dots' (max .06° of visual angle along edges), moving coherently in opposite directions. The direction of dot motion was either vertical (Fig. 1a and b) or horizontal (Fig. 1c and d). Animation frames were updated at 30 Hz, and the whole sequence of 25 frames was looped repeatedly to produce continuous motion. Maximum motion-speed of dots was 2.6° per second, and dot lifetime was four frames (120 ms). Dot density (quantified by the ratio of light to dark pixels) for each visible surface was 3% for all stimuli, with the exception of the opaque 'dense' stimulus used in Experiment 2 (see below), which had a density of 6%.

Cues for surface-curvature in depth were introduced by modulating both the speed and aspect ratio of dots as they moved along their paths. These two properties covaried as a consequence of the method used for generating the stimuli (i.e., by wrapping a flat sheet of random dots around a virtual 3D model of a cylinder or sphere, created in Matlab). In practice, these speed and aspect-ratio visual properties were held constant across the critical experimental manipulations, so they cannot confound our comparisons. As one example, to produce the appearance of a cylinder rotating around a horizontal axis, dots moving (vertically) towards the upper or lower edge (and thus in both the y-direction and also apparently in the z-direction orthogonal to the plane of the screen) would simultaneously decelerate and compress in the y-direction, reaching zero velocity and height at the edge of the cylinder (see Fig. 1a and b). Two different surface profiles were tested: cylindrical (Experiments 1 through 3) and hemispheric (Experiments 3 and 4). In each stimulus, dots moving in opposite directions could have different (or same) luminances from each other, allowing stimulus control over the appearance of translucency, opaqueness, or full-transparency for each cylinder or hemisphere.

In Experiment 1, the inter-dot Michelson contrast (between dots going in opposite directions) for the Context stimulus varied from 0% (transparent) though to 100% (opaque, i.e., now with only one direction of dots visible) in five linear steps of 25% (see examples of 0%, 50%, and 100% contrast in Fig. 2; see also supplementary material for animations). Dots in the opaque stimuli therefore had twice the luminance (80 $\mathrm{cd\,m^{-2}}$) as those in transparent stimuli, with the exception of the two control conditions in Experiment 2 (see below), in which the luminances were equated (i.e., both 40 $\mathrm{cd\,m^{-2}}$). Experiment 2 also included stimuli with just the extremes and the midpoint value of inter-dot contrast. In Experiment 4 only, binocular disparity was introduced by 'rotating' the left-eye and right-eye virtual stimulus hemispheres by 0.75° in opposite directions around their vertical axes (as if viewed from two different horizontally offset positions), resulting in a maximum horizontal disparity of 0.1° of visual angle. This produced a compelling impression of depth between front and back surfaces, projecting and receding respectively from the plane of the screen, thus making the apparent rotation in 3D less ambiguous, as confirmed experimentally below (see also Supplementary material).

Each display (except for unilateral conditions in Experiment 4, see below) comprised two RDK's. These comprised one Test stimulus, plus a Context stimulus, each presented on the horizontal meridian on either side of a small central white fixation dot (see Fig. 1a and c and Supplementary materials). Distance from the centre of one stimulus to the central fixation point was 3.15° for Experiments 1 and 2; 0.8° for Experiment 3. Stimulus dimensions for each 'cylinder' were 3.72° by 3.72°; 'hemispheres' measured 3.15° vertically by 1.57° horizontally in Experiment 3. The appearance of stereo-depth in Experiment 4 was slightly improved by scaling up the stimuli to 5.12° by 2.56° (now with 1.3° centre-to-fixation distance). The two stimuli in each display, one in each hemifield, always had the same type of surface profile (i.e., both cylinders or both hemispheres), and both had dot-motion vectors with the same vertical or horizontal orientation. By default, a perfectly transparent and thereby ambiguous test stimulus (with

a



Transparent Test

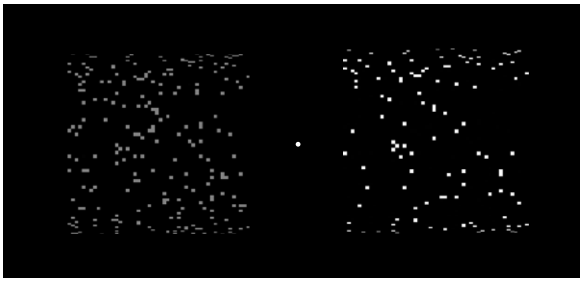
Transparent Context (0% contrast)

b

Transparent Test

Translucent Context (50% contrast)

c



Transparent Test

Opaque Context (100% contrast)

Fig. 2. Examples of displays with three levels of Context inter-dot contrast. Test stimulus is always transparent (i.e., 0% inter-dot contrast). (a) Transparent context (0% contrast). (b) Mid-translucent Context (50% contrast). (c) Opaque Context (100% Contrast). See also supplementary online animations corresponding to each of these examples.

dots in the two different directions having the same luminances) was presented on the left of fixation, and a context stimulus of variable translucency (with oppositely moving dots potentially having different luminances, see above) was presented on the right, in Experiments 1, 2, and 3. Since this left–right aspect was held constant across our manipulations, it should not confound our comparisons. Nevertheless, following advice from a referee, we fully counterbalanced the left/right positions of the context stimulus relative to the test stimulus in Experiment 4.

A further unique aspect of Experiment 4 was that we also included a unilateral 'long-epoch' condition, in which the different types of disambiguated 'context' stimuli were each presented alone on the left or right, with dot-motion (and thereby rotation) proceeding in a constant direction for the entire 40-s duration of each block in these unilateral conditions. This allowed assessment of any possible reversals in perception for a constant context stimulus over an extended time period. In all other conditions of that experiment (and throughout all the other experiments), the dots in the context stimulus periodically reversed their actual direction of motion, with intervals between reversals varying randomly between 3 and 6 s.

Increasing context opacity should generally reduce the ambiguity of context rotation, with the brighter set of dots tending to appear on the front surface, and the darker dots on the back surface (e.g., Schwartz & Sperling, 1983). For such stimuli (as also for the binocular-disparity context stimuli in Experiment 4), there were therefore two distinct *veridical* rotational states. For example, for stimuli with a horizontal axis of rotation, increasing the luminance of the upward-moving dots biased them to appear on the front surface (with the darker dots then appearing to move downward on the back surface), resulting in the perception of 'upward' rotation; alternatively the downward moving dots might be brighter, thus appearing on the front surface (with upward moving dots now appearing on the back surface), resulting in the appearance of 'downward' rotation. Likewise, for stimuli with vertically oriented rotational axes, the dominance of 'leftward' or 'rightward' rotation could be manipulated via the relative luminance of the leftward and rightward moving dots in the context.

For perfectly transparent contexts (equal luminance for the two overlapping directions of motion, 0% Michelson inter-dot contrast) without any binocular-disparity, dot reversals were still programmed and occurred for the context stimuli, but this direction of rotation was both subjectively and objectively ambiguous as there was no stimulus evidence to indicate the relative depth ordering of surfaces. Note, however, that for data analysis, the rotational state of transparent stimuli was still coded in the same way as for non-transparent stimuli, with one of the programmed surfaces arbitrarily identified as the 'front' throughout.

2.3. Design and procedure

Each experiment consisted of a series of 30-s (Experiments 1–3) or 40-s (Experiment 4) blocks, during which RDK's were continually presented on both sides of fixation (except for the unilateral long-epoch extended blocks in Experiment 4, see above). The observer's task was to make ongoing two-alternative subjective reports for both stimuli, using separate pairs of keys for each hand, and holding down one or other key on each side to indicate the currently perceived direction of rotation for that side. For the left hand, keys 'f' and 'v' (under second finger and index respectively) were used to indicate dominance of upward versus downward rotation for the left stimulus, respectively (or leftward versus rightward rotation, depending on the horizontal versus vertical rotational-axis orientation). Likewise for the right hand, keys 'j' and 'n' (under second and index fingers, respectively) indicated dominance of upward versus downward rotation, respectively, for right stimuli (or rightward versus leftward rotation). These instructions were easily grasped by all subjects, with the help of unambiguous opaque demonstration stimuli. At the end of each block, the screen remained blank until a keypress from the observer triggered the next block. Each experimental condition was repeated in random order a minimum of 10 times, over multiple 45-min sessions on separate days.

2.4. Data analysis

The binary states of left-hand keys and right-hand keys were each recorded concurrently with the veridical direction of rotation of the context stimulus, for every display frame. Each of these three time-series (i.e., current states of left response, right response, and of context stimulus on a particular side) were divided into stacks of individual epochs of identical duration, starting at each reversal of the context stimulus and ending 3-s later. Although in the experiment the actual time between successive context reversals varied between 3 and 6 s, this 3-s epoching of the data allowed mass pooling of responses regardless of actual epoch duration, thus increasing statistical power at the cost of discarding data collected outside these 3-s windows (i.e., after 3 s following a context reversal for those occasions where the next reversal took place later). This 3-s duration was chosen to be shorter than the average duration of perceptual stability, based on observations made during piloting. In Experiment 1 for example, mean spontaneous switch rate across subjects was 5.53 s (standard error 1.49). An alternative procedure that included data after the 3-s cut-off produced similar results but with reduced statistical power. The following analyses concern just the initial 3-s period following a veridical reversal of the context stimulus.

Each of the three time-series could be compared with each other, to derive three different measures of performance. First, comparison of those responses indicating perceived context-reversals against the veridical states of that context stimulus provided an objective measure of sensitivity to '*Veridical-Context*' reversals (i.e., the extent to which changes in the context stimulus led to changes in its perception). Coupling between these two time-series was quantified by counting the number of frames during which the states in the two streams were congruous (e.g., observer is indicating 'up' motion while the context is indeed such that the higher-contrast dots, or those with front stereo-disparity cues in Experiment 4, are those moving 'up'), and then calculating the proportion of such congruent frames out of the total number of frames in the 3-s epoch. A value of 0.5 would indicate that the two streams were independent, while 1.0 could only be achieved if the streams were identical. It was necessary of course to compensate in some way for response latencies, that would shift the two streams slightly out-of-phase, which could lead to an underestimate of coupling. The analysis procedure therefore first estimated each subject's individual average latency for responding to context reversals (for all inter-dot contrasts greater than 0%, i.e., excluding transparent contexts), by testing a range of possible phase offsets (up to 1 s) and choosing the offset for each subject that overall produced the maximum estimate of Veridical-Context dependency. The individual subject offsets were then applied to all further analyses for the other types of coupling (see below). Please note that this procedure cannot bias the results in favour of any of the critical conclusions below. For Experiment 1, the mean offset across subjects was 790 ms, SE = 45 ms; Experiment 2 mean = 829 ms, SE = 75 ms; Experiment 3, mean = 636 ms, SE = 28 ms; Experiment 4 mean = 744 ms, SE = 110 ms.

The resulting measure of Veridical-Context coupling, quantifying the extent to which subjective perception of the context stimulus correctly reflected the veridical reversals applied to it, should generally increase as a function of context opacity. Direction of rotation is completely ambiguous when the context is perfectly transparent, and should become progressively less ambiguous the more that inter-dot contrast indicates a specific depth-ordering of surfaces for context stimulus, with opaque stimuli lying at the other extreme. Three further different levels of translucency between these two extremes were introduced here, via the relative-contrast manipulation for the context stimulus (see above).

In addition to assessing Veridical-Context coupling, we also extracted a measure of coupling between *subjective* reports of the context stimulus and subjective reports of the test stimulus (as in Grossmann & Dobbins, 2003). A high value on this '*Context-Test*' measure would indicate that the stimuli were perceived to co-rotate and to reverse together. If the context state were always reported 'correctly', context-test coupling would provide a sufficient measure of how well the context stimulus drives reports for the test stimulus. However, as the context becomes more transparent, the tendency for reported context states to deviate from the veridical state should increase (since perception becomes progressively less constrained by the weakened relative luminance cues indicating which set of dots should be perceived as in front or most dominant). Under such conditions, Context-Test coupling might still remain high, if the test state tends to follow any spontaneous switches in the subjective context state (as observed in past studies of spontaneous coupling using a similar measure, e.g., Grossmann & Dobbins, 2003), which would then make the exact contribution of the veridical context-stimulus state difficult to determine.

This problem was circumvented here by extracting a third measure from the data, which compares test-report streams with veridical-context-*stimulus* streams directly. This comparison yielded our most critical '*Veridical-Test*' measure, of coupling between the state of the context stimulus (objectively determined) and perception of the test stimulus (subjectively reported). This provides an index of *stimulus-driven coupling* between changes in the context stimulus and reported perception for the ambiguous transparent test stimulus, corresponding to the proportion of frames during which the subjective appearance of the test stimulus matched the objective state of the context. This value should be higher than 0.5 if the veridical state of motion direction for the context consistently induces a corresponding subjective state for perception of the test stimulus motion. Note that its maximum value is likely to be limited by the objective detectability of the veridical switch (corresponding to our Veridical-Context score).

3. Experiment 1: Context translucency and axial alignment

This experiment manipulated context translucency over five equally spaced values between transparent and opaque (see above). A second, orthogonal factor manipulated the axial alignment of test and context cylinders. In the coaxial arrangement, cylinders rotated around a single horizontal axis, with their component dots moving vertically (see Fig. 1a and b for a schematic illustration of these stimuli, and also supplementary materials for animated demonstrations). In the non-coaxial arrangement, each cylinder was simply rotated around its centre by 90°, such that the dots now rotated horizontally around two separate vertical axes (see Fig. 1c and d).

The few studies that have manipulated axial alignment between a pair of SFM stimuli have produced discrepant results. Eby et al. (1989) reported a null effect, but Bonneh & Gepshtein (2001, abstract only) indicated tentative evidence for a positive effect, whereby collinear (coaxial) arrangements may have promoted 'spontaneous' coupling of perceived rotation direction. Finally, a recent study (Kanai, Moradi, Shimojo, & Verstraten, 2005) reported that a transient flash could induce subjective reversals when localised over an ambiguous SFM stimulus; in addition it could also sometimes induce a reversal in a second distant SFM stimuli, provided both were coaxial. However, in contrast to those studies, our measure of stimulus-driven coupling addressed the issue of whether the *specific* objective state of the context (rather than a non-specific flash, or else the subjective state of the context) can influence the specific subjective state of the test.

3.1. Results and discussion

Fig. 3 plots group means for seven observers in Experiment 1, for the three measures described above (i.e., coupling for Veridical-Context; Context-Test; and Veridical-Test, shown as proportion of frames with matching states). Error bars indicate one standard error. As expected, objective accuracy in discriminating veridical reversals in the direction of context motions (Veridical-Context, see Fig. 3c) increased rapidly from floor (0.5) to around ceiling with increased opacity (i.e., higher relative contrast between the two sets of oppositely moving dots in the context stimulus). The measure of subjective coupling between perceived directions of Context and Test rotations (Context-Test, see Fig. 3b) followed the reverse pattern, with maximum coupling for a transparent (and hence ambiguous) coaxial Context, gradually decreasing to a minimum as the Context became opaque (only one direction visible). This aspect of the results corroborates those reported by Grossmann & Dobbins (2003) with their similar measure of spontaneous coupling (see Section 8 of their paper for an experiment parametrically manipulating context translucency).

While the above measure of Context-Test coupling replicates past findings, our critical new measure of Veridical-Test coupling (Fig. 3a), between the subjective state of the

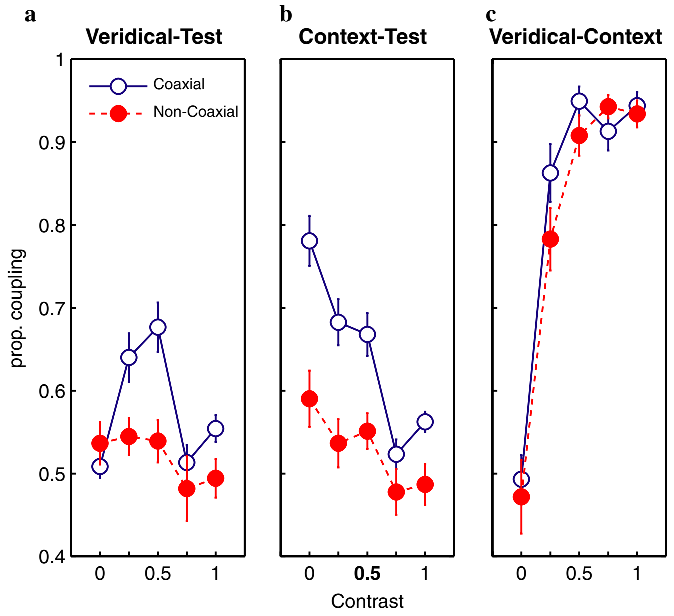


Fig. 3. Experiment 1 results: three measures of mean coupling across seven observers plotted against context inter-dot contrast, varying from transparent (0 on *x*-axis) to opaque (1). Unfilled symbols for Coaxial configuration; filled symbols for non-coaxial. Errorbars indicate one standard error. (a) Veridical-Test measure of stimulus-driven coupling between objective state of context stimulus and subjective state of test perception. Note that coupling increases to a maximum for mid-translucent context (i.e., significant coupling for 0.25 and 0.5 inter-dot contrast), but drops again to a minimum as opacity is approached (0.75 and 1.0). (b) Context-Test coupling between subjective percepts for the two stimuli. Note minimum coupling with opaque context, as in Grossmann and Dobbins (2003). (c) Veridical-Context coupling between the objective state of the context and its own subjective state (i.e., discriminability of veridical context reversals). Note ceiling performance for context discrimination for inter-dot contrasts values of 0.5 and greater.

test and the *actual* state of the context stimulus, reveals a new phenomenon of *stimulus-driven coupling*. For coaxial pairs of cylinders, stimulus-driven coupling was maximum for translucent contexts with intermediate 25% and 50% contrasts (see open symbols in Fig. 3a), though decreasing sharply to a minimum with contexts of 75% and 100% opacity. A further novel result here was that little or no strictly stimulus-driven coupling was observed for any transparency value with the non-coaxial stimuli (compare filled with open datapoints for the Veridical-Test graph in Fig. 3a); in addition, spontaneous subjective coupling in perceived rotation was also much weaker for the non-coaxial stimuli (compare filled with open datapoints for Context-Test graph in Fig. 3b).

The errorbars shown in Fig. 3 indicate the between-subject variability of these effects (corresponding to ±1 unit of standard error). We further assessed the statistical reliability of the critical Veridical-Test results (Fig. 3a) across subjects, in an ANOVA with context-contrast and axial-alignment as the two orthogonal, repeated-measures factors. There was a significant interaction between these factors [$F(4,24) = 5.46$, $p < .003$] as well as a main effect of context-contrast [$F(4,24) = 8.66$, $p < .0002$].

The above analysis of *stimulus-driven coupling* (Veridical-Test scores) quantifies the general tendency for subjective test-perception states to mirror the objective state of the context stimulus, during the 3-s window following a context switch. However, this state measure may not directly reveal any transient effects of context-stimulus switches upon test-perception *switches* per se (rather than on more enduring states). For example, stimulus-driven coupling might induce a test-perception switch following shortly after a context-stimulus switch, but this might not persist as an ongoing state. As pointed out by a referee, our state measure might thus conceivably underestimate any such highly transient coupling, if the test-perception state tended to decouple from the context-stimulus during the 3-s period after such an induced switch.

To assess switches per se, rather than states, we therefore next performed an additional analysis of the Veridical-Test time series, to evaluate the probability that a transient context-stimulus switch will induce an initial test-perception switch in the same rather than opposite direction. In Fig. 4a, results are graphed as the proportion of the total number of 3-s epochs (initiated by an objective context-switch) in which there was a subjective test-perception switch towards co-rotation, so that values of 0.5 indicate that either direction of switch (i.e., towards or against the switched context-stimulus) was equally likely. This discrete analysis of switch-specific coupling yielded slightly higher maximum estimates of coupling compared to the state measure (cf. Fig. 3a), but importantly only for the same translucent (intermediate 25% or 50% contrasts) and coaxial conditions for which we had found stimulus-driven coupling in the state analysis. In addition, some tendency was revealed for opaque (and near-opaque) non-coaxial cylinders to induce test-perception switches in the opposite direction of rotation (c.f. Gilroy & Blake, 2004); see dotted line and solid red points at right of Fig. 4a.

From this analysis we could also estimate the mean latencies at which the first subjective test switch occurred after a veridical context switch, here graphed separately for test switches towards (Fig. 4b) or away (Fig. 4c) from the current context-stimulus state. Subjects consistently showed latencies lower than 1.5 s (the mean predicted if a switch could occur at any time during the 3-s epoch) only for the coaxial, 25% and 50% contrast conditions, and then only for test switches *towards* rather than against the new veridical state of the context.

Thus all of these different methods of analysis indicate reliable stimulus-driven coupling imposed by the context stimulus, most notably and consistently for mid-translucent and coaxial contexts. Our subsequent experiments likewise found very similar results when considering either state-based or switch-based coupling analyses. For brevity we therefore present only the state-based results for the subsequent experiments.

At this stage, the results shown in Figs. 3a and 4a provide clear initial evidence that veridical changes in rotation direction for a mid-translucent context cylinder can reliably

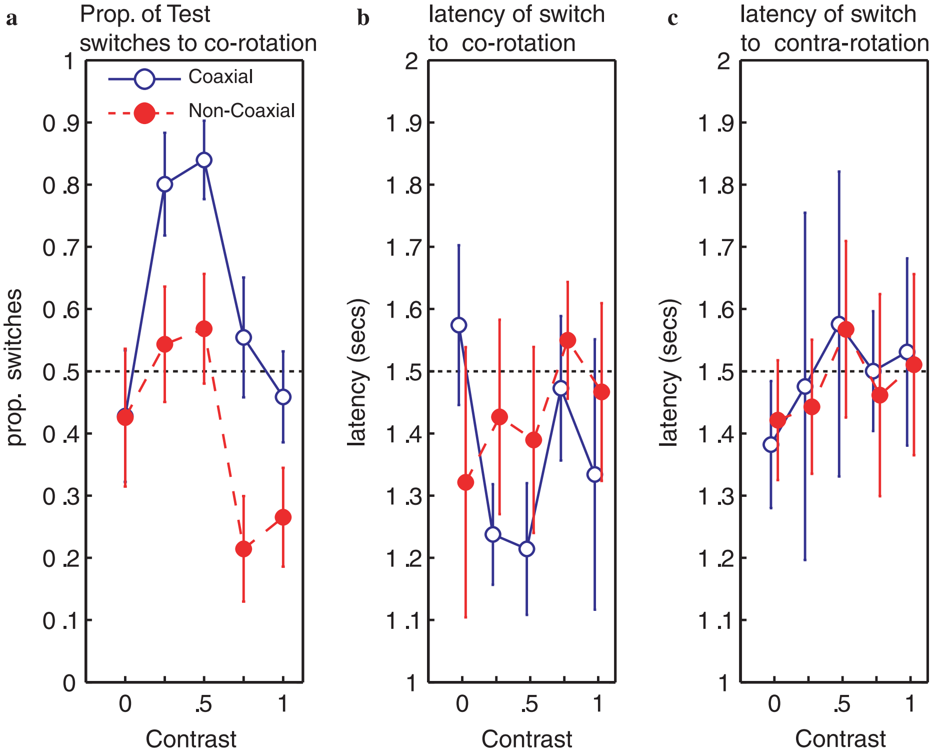


Fig. 4. Experiment 1 ($n = 7$), analysis of the first test-perception switches within each epoch. (a) Mean proportion of first test reversals that were in the same direction as the veridical context rotation (i.e., resulting in a state of perceived co-rotation between test and veridical context). Open symbols for coaxial configurations; filled symbols for non-coaxial configurations. Value of 0.5 (dotted horizontal line) corresponds to equal probability of a switch into a state of perceived co-rotation versus counter-rotation. (b) Mean latency (seconds) relative to epoch start, for first test-perception switches towards a state of co-rotation with the veridical context. (c) Mean latency of first test-perception switches into a state of counter-rotation. Note that for 3-s epochs, mean latencies of 1.5 s (dotted line in b and c) would correspond to a null effect of context switches on test switches. Error-bars indicate ±1 unit of standard error.

induce coupled subjective changes in perception for a coaxial transparent test cylinder. By contrast (and in general accord with Grossmann & Dobbins' (2003) study of purely spontaneous coupling, see the experiment in Section 5 of their paper), veridical switches in an *opaque* context did not induce stimulus-driven coupling here. Likewise, the 75% contrast context was also ineffectual at driving test switches, even though not opaque, however it is possible that any influence of the lower contrast direction may have been weakened by competition with the more salient 'front' surface.

The present observations of *stimulus-driven* coupling depended not only on context translucency, but also on the configural arrangement of the stimuli, being observed only when both the context and test stimuli share the same axis of rotation, a point to which we return in our third experiment. Our next experiment focused instead just on coaxial configurations, where Experiment 1 had found the most critical effects of context translucency.

4. Experiment 2: Context density and luminance

In Experiment 1, the opaque context had differed from the transparent test in two ways, as a result of the inter-dot contrast modulation used to generate them. First, the opaque stimuli had half the density of dots per unit area, because one whole surface of dots became invisible. Second, the dots that remained visible in the opaque context had twice the luminance of those in the test stimuli.

We therefore conducted a control experiment to test whether such low-level physical dissimilarities between transparent test stimuli and opaque context stimuli could, on their own, explain the failure of the opaque context to trigger subjective switches for a coaxial test stimulus. In a new 'Dim' condition, the luminance of this same opaque stimulus was halved, so that its dots now had the same luminance as the dots in the transparent Test stimulus (see centre illustration in Fig. 5a, and compare to the standard Opaque on the left of Fig. 5a). In the second 'Dense' condition, dots were added to the above 'Dim' opaque context to produce a stimulus that had double the density (see right of Fig. 5a). If the observed breakdown of coupling between coaxial cylinders when using an opaque context and transparent test was due merely to the low-level physical dissimilarities of those stimuli, then either or both of the new luminance or density manipulations might increase our Veridical-Test measure of stimulus-driven coupling in states, compared to the null value of 0.5 coupling obtained with the standard opaque context stimuli. For reference, we also replicated the opaque, mid-translucent (50% inter-dot contrast) condition and the transparent (zero inter-dot contrast) coaxial conditions from Experiment 1.

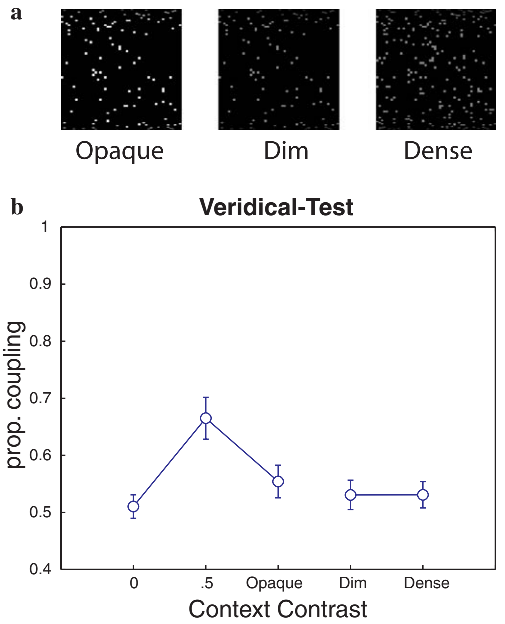


Fig. 5. Experiment 2, control stimuli and results. (a) Approximate appearance of opaque stimuli, from left to right: standard Opaque Context; 'Dim' with half the dot luminance of Opaque; 'Dense' with half luminance and double dot density. (b) Average Veridical-Test stimulus-driven coupling across eight observers, as a function of the three standard levels of Context inter-dot contrast and the two control conditions illustrated above. Errorbars represent ±1 standard error. Note that coupling was significantly above chance (0.5 proportion) only for mid-translucent stimuli (0.5 inter-dot contrast).

4.1. Results and discussion

Fig. 5b plots the critical Veridical-Test coupling results for eight observers (including three new subjects). These results clearly show no stimulus-driven coupling for any condition except the mid-translucent context, just as for the coaxial configurations in Experiment 1. Likewise, Bonferroni-corrected *t*-tests confirmed no significant deviation from 0.5 (i.e., null) coupling for any of the conditions except for the mid-translucent context (the latter comparison gave $t(7) = 4.5$, $p < .05$). The same outcome was found with an analysis of switch-specific coupling instead (see Experiment 1 for details of that approach). These results weigh against any explanation of the absence of coupling with opaque stimuli (versus presence of coupling with mid-transclucent) based merely on dissimilarity between stimuli in superficial aspects. Rather, the critical difference between opaque and mid-translucent stimuli may be simply whether just one surface or two surfaces are clearly visible.

5. Experiment 3: Axial-alignment versus opponent-motion or surface-interpolation

The results of Experiment 1 indicated that misalignment of rotational axes can apparently veto stimulus-driven coupling even in the presence of a mid-translucent context stimulus. Our next experiment tested the importance of higher-order versus lower-level explanations for this apparently configuration-dependent phenomenon. One important concern is that the axis-alignment manipulation in Experiment 1 might have led to some change in local motion energy. The two rotating cylinders in the axis-aligned condition of Experiment 1 (shown in Fig. 1a and schematically in Fig. 1b) had vertically moving dots, so dots from the different cylinders on the left and right did not approach each other. By contrast, the horizontally moving dots in the rotated cylinders from the non-coaxial condition in Experiment 1 (Fig. 1c and d) moved towards or away from the other cylinder (although never colliding). There is some evidence from physiology and functional imaging that motion-sensitive area MT can be relatively deactivated under such conditions of opponent motion, as if the local motion energies cancel each other out (e.g., Heeger, Boynton, Demb, Seidemann, & Newsome, 1999; Qian & Andersen, 1994; Snowden, Treue, Erickson, & Andersen, 1991). This might conceivably have weakened the motion signal associated with veridical context-reversals in the case of non-coaxial stimuli in Experiment 1.

To assess such possibilities, we now introduced 'hemispheric' stimuli (see Fig. 6 for schematics, and note that the black lines were not present, being shown here only to indicate possible axes of rotation). These hemispheric stimuli were arranged on the left and right of fixation so that they could appear to form a single rotating virtual 'sphere', with dots moving either vertically (Fig. 6a), or horizontally (Fig. 6b) around a common horizontal or vertical axis (respectively). Unlike the cylinders (cf. Fig. 1), there could

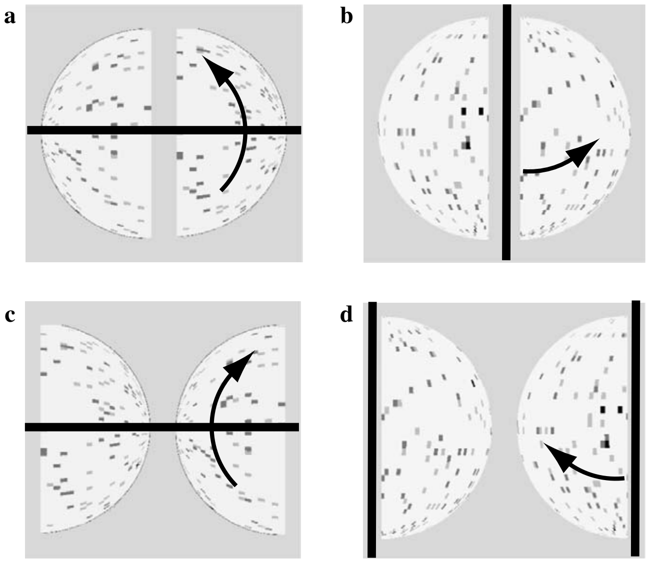


Fig. 6. Three-dimensional rendering of 'hemispheric' stimuli and configurations used in Experiment 3. (a) Left test and right context stimuli, each with vertical dot motion, arranged to form a 'sphere' configuration with shared horizontal axis of rotation. (b) Hemispheres with horizontal dot motion forming a sphere with shared vertical axis of rotation. (c) Rearrangement of vertical-motion hemispheres to form an 'hour-glass' configuration with a shared horizontal axis of rotation. (d) Horizontal-motion hemispheres in a similar configuration to (c), but now with independent vertical axes of rotation.

now be a common axis of rotation for both vertical *and* horizontal dot motions in these cases.

Despite often tending to appear as a single rotating spherical form (i.e., with perceptually coupling between hemispheres, see below), the two component hemispheres were just as independent in physical terms as the two cylinders used in the earlier experiments. Thus only one of the two concurrently present hemispheres was actually stimulus-biased to favour one direction of apparent rotation, undergoing veridical switches in dot-motion direction, while the other was completely ambiguous (fully transparent). In the cases of horizontal or vertical dot motion it was thus always possible for one hemisphere to appear de-coupled from the other, so that for example, the 'front' surface dots in one hemisphere would appear to move in the opposite direction to the other. Such de-coupled percepts were in fact spontaneously reported by observers, analogously to the cylinder case. Moreover, in pilot work with the hemispheric stimuli we found such de-coupling could be more frequent when using opaque contexts, though here we focus only on mid-translucent contexts.

If the above opponent-motion account of the Experiment 1 results were correct (i.e., opponent motion for horizontally moving dots disrupted coupling for non-coaxial cylinders), then with the new hemispheric stimuli coupling should also be abolished with horizontal dot motion for the same reason. Thus coupling should be observed only for stimuli like Fig. 6a but not Fig. 6b, analogously to those results already found for stimuli like Fig. 1a and b, but not Fig. 1c and d. However, if common-axis structure is instead the critical factor, similar coupling should now be observed for *both* vertical and horizontal dot-motion directions, because common-axis structure is preserved in both variants of the new hemispheric stimuli (Fig. 6a and b).

A second difference between the coaxial and non-coaxial arrangements used in Experiment 1 (Fig. 1) raises a further possible explanation of those configuration-dependent results, in higher-level surface-based terms. There is some evidence that a process of interpolation can construct a representation of a continuous surface that 'fills-in' the spaces between random dots in typical structure-from-motion RDK displays (e.g., Treue, Andersen, Ando, & Hildreth, 1995). The vertical edges of the two coaxial cylinders in Fig. 1a/b are coplanar, providing the possibility of interpolating a continuous surface that bridges the gap between them. The present stimulus-driven coupling effects, and the configural dependency found in Experiment 1, might therefore potentially depend upon propagation of contextual information across such an interpolated surface, even if that surface itself is invisible (i.e., perceived to be either transparent, or opaque black against a black background). On such a surface-interpolation account, coupling might fail for two non-coaxial rotating cylinders (see Fig. 1c and d) because the central gap between their facing convex surfaces cannot be bridged or interpolated across in the same way.

In the present Experiment 3, we sought to disentangle axial-alignment from the surface-interpolation possibility just described (and from motion-opponency, see above), by using hemispheric stimuli similar to Fig. 6a and b above, but now reversing their left–right order to produce 'hourglass' configurations (see Fig. 6c and d). This arrangement produces a clear surface-discontinuity, but still allows dot-motion direction (vertical or horizontal) to be used to manipulate axial alignment independently. Now only vertical motion is consistent with a single common axis of rotation (Fig. 6c); in contrast, horizontal motion would suggest two separate (vertical) axes of rotation (as marked schematically with black lines in Fig. 6d), just as for the non-axial cylinders shown schematically in Fig. 1d. If the stimulus-driven coupling we have discovered critically depends upon axial structure rather than surface continuity, coupling should still be observed for the hourglass configuration with vertical dot motion (where axial alignment is preserved, see Fig. 6c), but not for horizontal dot motion in this configuration (where axial alignment is disrupted see Fig. 6d). However, the surface-continuity hypothesis would predict no coupling for either direction of motion in the hourglass configuration where surface-continuity is disrupted (Fig. 6c and d), in contrast to both directions for the sphere configurations where it is preserved (Fig. 6a and b, see above).

In comparison with the two alternative accounts discussed above ('surface-interpolation' and 'opponent-motion'), the axial-alignment hypothesis thus makes a unique prediction: coupling should be observed in all cases *except* for horizontal motion in the hourglass configuration (i.e., Fig. 6d), which is the only stimulus in which axial alignment is disrupted. Note that the above stimulus manipulations effectively orthogonalize the two factors of surface-continuity and motion-opponency, resulting in a 2×2 factorial design. Thus we may independently assess the effects of each factor independently (as presumably additive main effects). Moreover the specific axial-alignment hypothesis may be tested by examining the interaction effect between the two factors.

As we were now concerned only with the effects of these specific configural issues upon stimulus-driven coupling, we only used the 50% context contrast (i.e., mid-translucent) in this new experiment, at which we had obtained the highest values of Veridical-Test coupling in the two previous experiments.

5.1. Results and discussion

Fig. 7 presents the mean veridical-test coupling scores for 7 new naïve observers, for whom dot-motion direction (horizontal or vertical, as in Fig. 6a and c, versus 6b and d) was manipulated in separate sessions in counterbalanced order, so as to minimise any interference between left–right versus up–down response-mappings. Mean objective discrimination of context reversals (Context-Veridical scores) was around 90% for all conditions, with this good

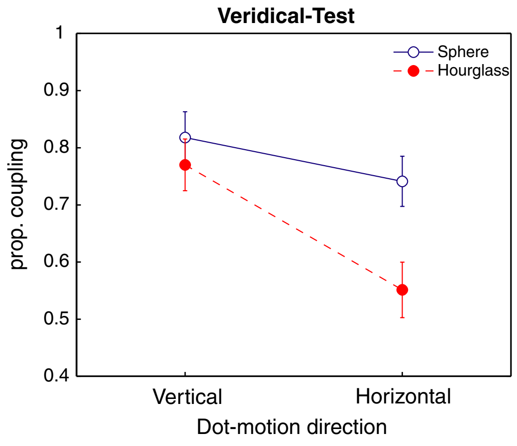


Fig. 7. Mean stimulus-driven Veridical-Test coupling across seven observers in Experiment 3, plotted for hemisphere stimuli with vertical or horizontal dot-motion. Unfilled symbols: 'sphere' configuration; filled: 'hour-glass' configuration. Errorbars represent ±1 standard error.

performance as expected given the mid-translucent contexts now used throughout this experiment (unlike the more transparent contexts that were included also in Experiments 1 and 2, whose rotation was harder to judge). This reliability of discriminations for veridical context states also meant that Context-Test coupling between subjective context perception and subjective test perception closely mirrored the critical Veridical-Test coupling (Fig. 7) between the context *stimulus* and the test percept. The latter data reveal that axis-alignment does appear to be a constraint on stimulus-driven coupling, since such coupling was found for the three arrangements depicted in Fig. 6a–c, but not for that shown in Fig. 6d, the one case where rotation was not around a single common axis.

The Veridical-Test data were analysed in a 2 × 2 repeated-measures ANOVA with the following orthogonal factors (cf. Fig. 6): dot-motion direction (vertical or horizontal) and surface continuity arrangement (sphere or hour-glass). The main effect of surface continuity was not significant [$F(1,6) = 3.33$, *ns*]. Vertical dot-motion (which was non-opponent) produced significantly more stimulus-driven coupling overall [$F(1,6) = 66.5$, $p < .001$], but importantly this was qualified by the significant interaction term [$F(1,6) = 21.76$, $p < .003$]. Bonferronni-corrected t-tests confirmed that all conditions except hourglass with horizontal motion (Fig. 6d, bottom right datapoint in Fig. 7) produced significantly greater than null (0.5) coupling (at $p < .05$ or better).

Neither opponent-motion nor surface-continuity (as described above) can on their own account for the full-pattern of results when considered as independent additive factors. It remains logically possible that some non-linear combination of these factors may operate (e.g., surface continuity might completely override all effects of opponent-motion in Fig. 6b). However, a potentially more parsimonious explanation of the interaction effect would be in terms of axial alignment, which by our design is uniquely disrupted in stimulus 6d compared to the other three configurations. The overall pattern of results in Experiment 3 is therefore consistent with our hypothesised critical role of axis-alignment, as opposed to motion-opponency or surface-interpolation operating in isolation.

6. Experiment 4: Eliminating residual ambiguity for mid-translucent contexts

The results so far show that strong stimulus-driven coupling can be induced by a mid-translucent context that is itself sufficiently disambiguated to yield ceiling levels of veridical rotation discrimination in the present paradigm (see the Veridical-Context measure for mid-translucent 25% and 50% contexts in Experiment 1, Fig. 3c). This result appears to weigh against Grossmann & Dobbins' (2003) proposed ambiguity-dependent-feedback account, that predicts poor coupling with relatively unambiguous contexts.

Nevertheless, as pointed out by a referee, it might be an overstatement to assert that the relatively unambiguous mid-translucent contexts driving maximum coupling thus far were as truly 'unambiguous' as the opaque context stimulus with which coupling fails. A defender of the Grossmann & Dobbins (2003) perspective might still argue that there could be some residual ambiguity in the mid-translucent context, thus better fulfilling the conditions for coupling according to the ambiguity-dependent-feedback hypothesis. If the mid-translucent context stimulus were indeed more ambiguous than the opaque, this should manifest as a tendency for spontaneous subjective switching of the context percepts, given sufficient viewing time. However, any such tendency might have been underestimated here so far, due to the occurrence of veridical context switches every 3–6 s, which meant there were only short epochs with a constant context stimulus. Possible perceptual reversals (implying some residual degree of ambiguity) might be revealed during more prolonged viewing of continuously rotating stimuli (i.e., with no veridical switching). Indeed, such spontaneous switching was observed by Grossmann & Dobbins (2003), with their continuously rotating translucent stimuli.

To address this, we took the standard translucent stimuli and added redundant *binocular-disparity* to reinforce the perceived separation of 'front' and 'back' surfaces into different depth planes (our thanks to an anonymous referee for inspiring this variation). We set out to test whether subjective percepts of an ambiguous test stimulus could become coupled with such a context stimulus that should be perfectly stable even under prolonged viewing, as we confirmed by direct measurement (see below).

Experiment 4 had two parts. In one part, concerned with quantifying the ambiguity of our different types of context stimuli, we measured subjective rotation-percepts for a single, unilateral mid-translucent hemisphere (presented in either hemifield in randomised order, with the vertical edge furthest from fixation, like half of Fig. 6c). In these 'unilateral-long-epoch' conditions, a single stimulus rotated constantly in the same direction around a horizontal axis throughout the entire duration of each extended 40-s block (with the ‘up’ versus ‘down’ direction of rotation chosen pseudo-randomly for each block, see also Section 2 above). Note that these blocks were 10 s longer than in the previous experiments, to test for the occurrence of any spontaneous perceptual reversals over more prolonged viewing of a constantly rotating stimulus.

We studied three kinds of stimuli. First, for comparison, we used our standard mid-translucent context stimulus (50% Michelson inter-dot contrast between directions again, viewed dichoptically with zero binocular disparity). Second, we now also included new stereo-depth translucent context stimuli, which had a redundant combination of binocular-disparity cues and luminance-based translucency cues to depth (i.e., translucency-plus-disparity, see supplementary materials for an animated demonstration for viewing with red-green glasses). Third, we tested a perfectly transparent stimulus with the same binocular disparity cues now added in isolation (i.e., transparent-plus-disparity), to see whether context disparity alone was sufficient to drive the test stimulus (see Section 7 for the implications of this). We anticipated that adding disparity should produce a highly unambiguous context stimulus in terms of perceived rotation direction, for which perception of 3D rotation should remain stable even over very extended viewing.

In the second part of the experiment (run in counterbalanced order), these three types of context stimuli were also tested in our standard paradigm for measuring stimulus-driven coupling (40 s blocks each comprising short-epochs with objective context reversals every 3–6 s), using the same ‘hourglass-with-vertical-motion’ configuration (see Fig. 6c) as used in Experiment 3 (in order to eliminate coupling mechanisms based on surface interpolation), but now with the left–right positions of context and test stimuli fully counterbalanced between blocks (see Section 2). While context stimuli were viewed dichoptically, the test stimulus was always viewed monocularly, through just the left eye (with a blank field presented to the right eye for the corresponding locations). This was intended to avoid ‘pinning’ those stimuli to any particular disparity-defined plane (c.f. Fang & He, 2004, see also Section 7).

A reduction of stimulus-driven coupling when using a less ambiguous context (with added disparity cues to bias perception of context rotation) should presumably be expected from Grossmann & Dobbins’ (2003) general proposal that less ambiguous contexts induce less coupling. By contrast, based on our previous experiments here, we would now predict such stimulus-driven coupling to remain or even to increase when disparity was added to disambiguate the context further, given that (unlike the opaque situation) both the front and back surfaces remain fully visible for the new translucent contexts with added disparity cues.

6.1. Results and discussion

In the unilateral-long-epoch conditions, the tendency for subjective reports to follow the objective direction (which was now constant throughout each 40 s unilateral block) was quantified for five naïve observers (three new), as the proportion of the total number of frames in each epoch for which the veridical direction was reported (i.e. analogous to the Veridical-Context measure in the earlier experiments). The standard mid-translucent stimulus (without disparity) yielded scores that were significantly above 0.5 (indicating some veridical perception), but still well below 1.0, indicating that under prolonged viewing (40 s epochs), subjective percepts could spontaneously reverse, thus overriding the luminance cues indicating the relative depth (see Fig. 8a, left bar). In contrast, stimuli with redundant disparity-plus-luminance depth-cues produced scores at ceiling values of 1.0 for all observers (i.e., with no spontaneous reversals over 40 s), indicating that these stimuli were perfectly unambiguous, as we had expected (Fig. 8a, middle bar). Transparent stimuli with disparity-cues alone (i.e., without redundant luminance cues to depth) showed few spontaneous reversals with prolonged viewing, although these did occur rarely (Fig. 8a right bar). Differences between the three conditions were significant overall [$F(2,8) = 6.89$, $p < .02$], with more spontaneous reversals in the absence of disparity cues ($p < .05$ by one-tailed Bonferroni-corrected t-test for the zero-disparity condition against each of the disparity conditions), as would be expected, though there was no significant difference between the two disparity conditions themselves.

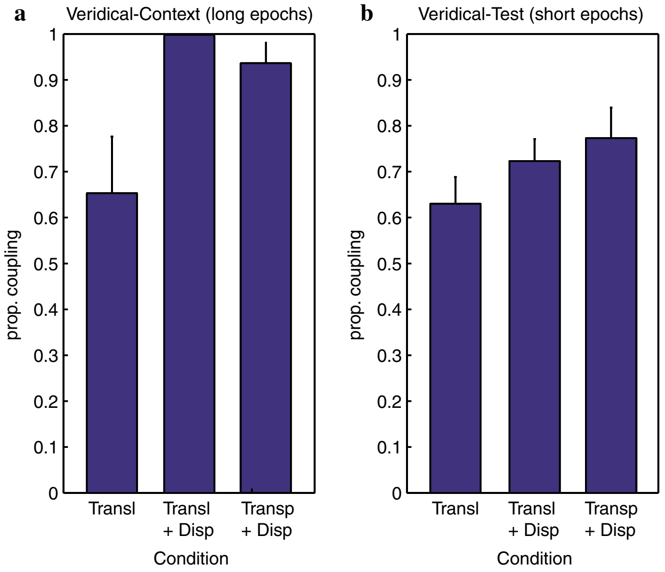


Fig. 8. Experiment 4 results from five observers. Within each plot, the left bar shows data for translucent context with zero disparity; the middle bar represents translucent contexts with redundant disparity-cues added; and the right bar represents transparent contexts biased only by disparity cues. (a) Veridical-Context coupling between the objective state of the context and its own subjective state, when viewed unilaterally without any veridical context reversals over extended epochs of 40 s. Note that contexts with disparity added are less ambiguous (i.e., less reversible), and that the translucent context with redundant luminance and disparity cues never showed any perceptual reversals, i.e., was always perceived correctly. (b) Mean Veridical-Test coupling between a monocularly viewed transparent test and periodically reversing (short epoch) veridical context. Note the higher coupling induced by the contexts with disparity cues added (right two bars in b).

Critically, when using these same three types of context stimuli but now within our short-epoch coupling paradigm (i.e., with context and monocular transparent test stimulus on opposite hemifields, with left/right positions counterbalanced; configuration analogous to Fig. 6c), we still found reliable stimulus-driven coupling on the Veridical-Test measures (see Fig. 8b). All three types of context stimulus produced more stimulus-driven coupling than the chance proportion of 0.5 congruence between the state of the context-stimulus and the perceived state of the ambiguous test, at $p < .05$ or better. Moreover, both conditions in which context ambiguity was reduced by disparity cues (cf. Fig. 8a) produced significantly *more* stimulus-driven coupling than the zero-disparity context ($p < .05$ in one-tailed Bonferroni-corrected pairwise *t*-tests), though the disparity conditions did not differ significantly from each other in terms of stimulus-driven coupling.

Notably, the context with redundant luminance and disparity cues to depth (i.e., translucent-plus-disparity, middle bars in Fig. 8) produced highly reliable stimulus-driven coupling [$t(4) = 5.2$, $p < .005$, middle bar in Fig. 8b] even though it was totally unambiguous, in the sense that counter-veridical switches were never reported despite the prolonged viewing periods (middle bar in Fig. 8a). This provides further compelling evidence against the proposal that less ambiguous contexts will invariably produce less coupling (cf. Grossmann & Dobbins, 2003).

The results for Experiment 4 are in general accord with Fang & He (2004), who found some stimulus-driven coupling between a disparity-biased context and a monocular test stimulus when these abutted. However, our present use of hour-glass stimuli (with a visual chasm between hemispheres) as opposed to abutting cylinders (as in Fang & He's, 2004 study) goes further than their study, in ruling out the possibility that this disparity outcome merely reflects the interpolation of very local binocular-disparity codes between closely contiguous surfaces. The present results support instead a coupling mechanism based on longer-range information sharing, in accord with our other three experiments, a point to which we return below.

7. General discussion

The phenomenon of coupling of ambiguous percepts (whereby multiple bistable stimuli often seem to flip between one or other perceptual interpretation together), has often been taken as evidence for *information-sharing* between distinct stimulus representations, which may impose global constraints upon local ambiguities. A recent challenge to this interpretation was posed by Grossmann & Dobbins (2003), whose observations of good spontaneous coupling between two ambiguous stimuli contrasted with a striking breakdown of coupling when one stimulus was rendered *un*ambiguous. However, as we pointed out in Section 1, many prior observations on perceptual coupling (including those of Grossmann & Dobbins, 2003) could in principle be explained away by stochastic variations in *internal noise*. This might explain not only spontaneous coupling between ambiguous stimuli, but potentially also the apparent lack of coupling with *un*ambiguous stimuli as reported by Grossmann & Dobbins.

The present study has provided critical new evidence for a type of *stimulus-driven* coupling between separate stimuli, which may arguably be explained only in terms of information-sharing. Critically, we were able to demonstrate that the perceived rotation of an ambiguous SFM 'test' stimulus could be driven by objective rotation-reversals of a separate, disambiguated 'context' SFM stimulus, using random-dot kinematograms to produce the impression of rotating three-dimensional cylinders or hemispheres (c.f. Andersen & Bradley, 1998; Grossmann & Dobbins, 2003; Nawrot & Blake, 1991; Treue et al., 1991). This phenomenon of stimulus-driven coupling was revealed by our 'Veridical-Test' measure, which quantified the correlation of subjective reversals of the test stimulus with objective reversals of the context stimulus.

The present findings of stimulus-driven coupling cannot be explained away solely by the internal-noise account, according to which (by definition) subjective switching and coupling phenomena should be driven only by stochastic internal events, not objective external events, as here. Moreover, our results seem to present a challenge to Grossmann & Dobbins (2003) proposed ambiguity-dependent-feedback account, according to which an unambiguous context should produce minimum coupling. Our studies demonstrate that (within specific boundary conditions) a context could induce reliable coupling even when it was effectively disambiguated via the manipulation of translucency and/or binocular depth cues. In Experiment 1, for instance, we found peak stimulus-driven coupling with mid-translucent contexts, which were sufficiently disambiguated to allow discrimination of veridical switches at near ceiling levels of accuracy, as measured within the same experiment (see Fig. 3c). For context stimuli approaching opacity (e.g., 75% opacity) coupling dramatically reduced to the levels observed by Grossmann & Dobbins (2003) with their opaque contexts, but resulted in no further increase in veridical discrimination. However, adding disparity-cues to translucency cues in Experiment 4 to further disambiguate the context stimulus (with the result that it was perceptually stable over 40 s of extended viewing) induced even stronger stimulus-driven coupling. The common property of the effective inducing contexts was that they were all translucent with 'front' and 'back' surfaces clearly visible, rather than opaque (or near opaque, where the effectiveness of the low-contrast surface may possibly have been inhibited in competition with the high-contrast surface). Thus the peculiar ineffectiveness of opaque (and near-opaque) stimuli in inducing coupling (as observed here, and also previously for opaque stimuli by Grossmann & Dobbins) may represent an unusual exception rather than illustrating any general rule associating coupling with context ambiguity.

While the present study shares some basic similarities to Grossmann & Dobbins' (2003), other differences in the methodology and the outcomes have led us to very different conclusions. In their first experiments (see their Experiments 1c and 1d), Grossmann & Dobbins did briefly mention some residual tendency for 'spontaneous' coupling with an unambiguous stimulus (i.e., between the subjective appearance of both stimuli, rather than for stimulus-driven coupling, as here). However, as they only examined opaque versus transparent contexts in that experiment (rather than mid-translucent stimuli as studied here), their main emphasis was on how coupling was *reduced* with the opaque stimulus compared to when both stimuli were ambiguous (a result which we also replicated in our Experiments 1 and 2), thus apparently supporting the ambiguity-dependent hypothesis. In their second main experiment (see Section 5 of their paper), they also objectively switched the state of the context (as we did here), though they did not report a measure corresponding to our 'Veridical-Test' coupling. However, they only used opaque contexts in that experiment, and consequently observed no effect of the context driving the ambiguous test, thus apparently supporting their theory further. In a further experiment (see their Sections 8 and 9) they parametrically reduced context translucency, as we did, finding a monotonic decline in spontaneous coupling (as we also did with our 'Context-Test' measure in Experiment 1). However they included no objective context switching, and thus were unable to distinguish stimulus-driven coupling from internally-driven spontaneous coupling.

By virtue of these differences to Grossmann & Dobbins' (2003) study, our study reveals for the first time clear stimulus-driven coupling with mid-translucent contexts, though evidently subject to specific constraints of surface visibility and axial alignment. It might be objected, however, that even this strictly *stimulus*-driven coupling might reflect small eye-movements, shifts of attention, or other generic internal changes triggered by veridical reversal of the context stimulus. For example, Kanai et al. (2005) found that a localised transient event (such as a flash) could induce a subjective reversal in SFM rotation, which sometimes also induced reversals in a distant coaxial stimulus (though note this sometimes resulted in counter-rotation rather than co-rotation, see their Experiment 3). Alternatively, feature-based attention (Saenz, Buracas, & Boynton, 2002; Treue & Martinez Trujillo, 1999) might conceivably be captured by the relatively brighter dots among the context dots here, perhaps especially when these reverse direction (though note this particular argument cannot apply for transparent contexts with binocular-disparity, which were also found to be highly effective inducers in the present Experiment 4). Feature-based attention might enhance the salience of similar motion, thus potentially biasing the perceived motion of the ambiguous test stimulus. However, any general account in these terms does not naturally explain the high specificity of our present findings: in particular, why small linear changes in inter-dot contrast from translucent towards opaque have such a dramatic and non-linear effect upon perception (see Fig. 3a); and why stimulus-driven coupling was so strongly constrained by axis-alignment (Figs. 3 and 7). Moreover, it would remain unclear why any such mechanism based on feature-based attention (or indeed transient-induced reversals, Kanai et al., 2005, see above) would not be maximally effective at promoting coupling with opaque context stimuli, rather than minimally effective as found.

By eliminating general explanations based on non-specific internal variables or feature-based attention, our results provide firmer grounds for suggesting that long-range stimulus-driven SFM coupling can reflect sharing of specific information between representations of context and test stimuli via which the less ambiguous state of one can bias the ambiguous state of the other. Moreover, our results provide some clear counterexamples to Grossmann & Dobbins' (2003) proposal that less ambiguous contexts invariably produce less coupling with ambiguous test percepts (which might itself have been explained away by the internal-noise account in any case, see Section 1). Our results also go beyond other past studies in four further respects: by showing stimulus-driven coupling between separate non-contiguous surfaces; and by illustrating the specific roles played by stimulus configuration, binocular disparity, and surface visibility. These observations provide some further pointers regarding the nature of the information that is exchanged and integrated in stimulus-driven coupling.

On the first of these points, there have been a few interesting reports in the literature of context-induced influences on subjective test perception for closely abutting or overlapping stimuli (Eby et al., 1989; Fang & He, 2004; Gilroy & Blake, 2004; Ramachandran et al., 1988). Coupling has been reported between more separated stimuli, but typically only for spontaneous (i.e., *not* stimulus-driven) coupling between ambiguous stimuli (Bonneh & Gepshtein, 2001; Eby et al., 1989; Gillam, 1972; Grossmann & Dobbins, 2003). Thus a novel contribution here was our demonstration that disambiguating contextual information can induce stimulus-driven coupling across a gap between SFM stimuli of up to 3° (the largest separation tested here, in Experiments 1 and 2); moreover, this information can bridge a visual chasm between two facing hemispheres with non-contiguous surfaces (i.e., in the 'hour-glass' configuration; see Experiments 3 and 4, and Fig. 6c).

This latter point may be important for ruling out a surface-interpolation explanation of long-range stimulus-driven coupling, whereby information might propagate from inducing stimuli across the visual field, but might tend to be constrained by edges, surfaces or other sensory discontinuities (Grossberg, 1994; Grossberg & Swaminathan, 2004; Hildreth, Ando, Andersen, & Treue, 1995). For example, local propagation of this type might explain the recent findings of Fang & He (2004) that subjective switches in the rotation of a monocularly viewed RDK cylinder can be stabilised by adding binocular disparity to dots at the edges of the same cylinder, as if the disparity information propagates laterally into the adjacent monocular region. Such interpolation processes might in principle also explain why, in Experiment 1, we found good coupling between the coplanar surfaces of coaxial cylinders, but not for the non-coplanar surfaces of non-coaxial cylinders. However, in our coaxial hour-glass configuration (see Experiment 3 and Fig. 6c), there was a substantial visual chasm between the two stimulus hemispheres, yet robust coupling was still observed (see also Experiment 4). Local propagation of surface information across coplanar surfaces therefore appears insufficient to explain all the cases of coupling observed here.

A second novel finding is the importance of stimulus configuration on stimulus-driven coupling in Experiments 1 and 3. The ambiguous test stimulus may have to share the same axis of rotation as its inducing translucent context stimulus, in order for robust co-rotational coupling to occur (see results in Figs. 3, 4 and 7). In Experiment 3, using the new hemispheric stimuli, we showed that this constraint is unlikely to reflect the factors of opponent-motion or surface-interpolation alone (at least when considered as separate additive factors, see above), as stimulus-driven coupling was still found in conditions that should have disrupted surface continuity (as in the coaxial ‘hour-glass’ configuration in Fig. 6c), and also in other conditions that should have included opponent motion (e.g., Fig. 6b). Coupling was only eliminated when there were two separate axes for possible rotation rather than one common axis (see Fig. 6d). Previous studies have appeared to conflict on whether configural factors constrain SFM coupling (e.g., see Bonneh & Gepshtein, 2001; Eby et al., 1989; and commentary by Grossmann & Dobbins, 2003), possibly because they used measures of *spontaneous* perceptual coupling. In contrast, here we observed strong effects of coaxial alignment on *stimulus-driven* coupling.

In principle, this configural influence might be guided by learned contingencies, relating to the probability of spatially separate stimuli in different configurations being actually causally connected (Gilroy & Blake, 2004). As one compelling example of how learned contingencies might play a role in contextual interactions, Gilroy & Blake (2004) recently showed that two RDK spheres (one ambiguous, the other not) with parallel axes appeared to counter-rotate only when touching each other, as if their behaviour were governed by the physical laws of friction. They specifically showed an increase in perceived *counter*-rotation induced by *opaque* context stimuli when rotating with *parallel* axes (with decreased counter-rotation for collinear axes), found when stimuli were *touching*. While there is some hint in our transient analysis of switches for Experiment 1 (see Fig. 4a) of a weak replication of this with more distant stimuli, note that our critical new results are very different; namely, increased *co*-rotation induced by *mid-translucent* (but not opaque) context stimuli, only when rotating with *collinear* axes, despite relatively large stimulus *separation*. Despite these gross differences, a similar account based on learned contingencies might suggest that the coupling of two coaxially rotating ‘hour-glass’ hemispheres (Fig. 6c) could be a plausible percept, for despite their surface discontinuity, the stimuli can still be seen as a parts of a single rigid object sharing a common fate.

In addition to addressing critical issues about contextual ambiguity in the present studies (see above), our manipulation of binocular disparity in Experiment 4 may also help to address an apparent discrepancy in the literature concerning whether long-range coupling can be induced by a purely disparity-biased context. Grossmann & Dobbins (2003, see their Experiments 1a and 1b) reported *null* coupling with a separated disparity-biased context. In contrast, however, Fang & He (2004) found good contextual disambiguation from an abutting transparent disparity-biased context. It was possible that Fang & He’s (2004) result may have merely reflected propagation of strictly *local* disparity codes between contiguous surfaces, which might then have explained the null-coupling observed by Grossmann & Dobbins (2003) with non-contiguous stimuli. This explanation now appears ruled out, however, given that the present Experiment 4 clearly showed that longer-range information-sharing can arise for a purely disparity-defined coupling effect (as for the transparent-plus-disparity context in our Experiment 4). An alternative explanation for the discrepancy in prior results may be that in Grossmann & Dobbins’ disparity study, both eyes viewed identical test stimuli (hence with zero-disparity); this was unlike Experiment 4 and Fang & He’s study, where test stimuli were only viewed monocularly. That aspect of Grossmann & Dobbins’ (2003) disparity experiment might have prevented coupling, by introducing a disparity-contrast between the (non-zero-disparity) context and the (zero-disparity) test stimulus (see Fang & He, 2004 on this point). But whatever the explanation, our results successfully extend Fang & He’s (2004) observation with contiguous binocular-disparity contexts, to a situation with *non*-contiguous stimuli, consistent with longer-range information-sharing.

Perhaps the most intriguing aspect of our results is the critical dependence of stimulus-driven coupling on context mid-translucency. In all four experiments, we found robust stimulus-driven coupling induced by relatively unambiguous mid-translucent contexts (with front and back surfaces both clearly visible). However, as also reported by Grossmann & Dobbins (2003), opaque contexts remained strikingly ineffectual at inducing coupling (both for spontaneous coupling and for stimulus-driven coupling as additionally measured here). Our present findings with mid-translucent contexts suggest that the case of opaque (and near-opaque, i.e., 75% contrast) contexts may be just an interesting exception to the more general rule that good coupling can be achieved with contexts that are effectively unambiguous (as indicated by observers’ ceiling performance in discriminating veridically different states). Experiment 2 further showed that the inability of opaque contexts to induce coupling could not readily be explained by low-level dissimilarities in dot density or luminance per se. Taken together, our results suggest a new fundamental *visibility constraint*, whereby both ‘front’ and ‘back’ surfaces of the context stimulus must be clearly visible for coupling to occur in SFM.

This visibility constraint seems to challenge the intuition that the two visible surfaces of a transparent SFM stimulus are represented in a co-dependent, mutually antagonistic fashion. Such an assumption is central to several prevalent models of SFM processing (Andersen & Bradley, 1998; Nawrot & Blake, 1991), implying that if one surface appears convex and in the foreground, the other surface must as a corollary be interpreted as concave and in the background. Such models would apparently predict incorrectly that a *single* surface visible in an opaque context should be able to simultaneously disambiguate *both* visible surfaces of the test stimulus. Our proposed visibility constraint suggests that the underlying assumption of reciprocal co-dependence may need to be revised.

Our data may fit better with an alternative account, recently proposed by Hol, Koene, & van Ee (2003), which suggests that each of the two visible surfaces of a transparent SFM stimulus may be represented *independently* from each other, rather than as one ensemble. This accounted for their own observation that their SFM stimuli (similar to the cylinders used here) could sometimes be perceived as having two convex ‘fronts’ or two concave ‘backs’, rather than always appearing as a cylinder with complementary front and back surfaces. Hol et al.’s (2003) independent-surfaces perspective may also account naturally for why, in the present study, a *single* visible context surface (as in opaque stimuli) cannot simultaneously disambiguate both visible surfaces of the test stimulus, and thus induce coupling. Each visible test surface may need *its own* clearly visible disambiguating context surface. This independent-surfaces theory may reconcile within a single explanatory framework all three of the coupling phenomena we have addressed: stimulus-driven coupling with mid-translucent and/or disparity-biased contexts (as clearly established here); spontaneous coupling between transparent stimuli (as previously shown); and the surprising de-coupling with an opaque context (as shown both here and in Grossmann & Dobbins, 2003).

Whatever the ultimate explanation of the proposed ‘visibility constraint’ on context-induced coupling between surfaces, our data unequivocally establish that mid-translucent and opaque contexts behave very differently. The latter induce no coupling, whereas the former can induce very robust coupling even when (as for the cases of binocular-disparity in Experiment 4) they are made highly *un*ambiguous. Thus, opaque contexts may prove to be the exception, rather than reflecting any general rule that less ambiguous contexts always induce less coupling, which we overturned here.

In conclusion, the stimulus-driven coupling we observed provides robust evidence for relatively long-range information-sharing between representations of distinct SFM stimuli. This new coupling phenomenon is neither readily attributable to internal stochastic noise, nor to general feature-based attention. Rather, stimulus-driven coupling seems to reflect contextual integration that can help to resolve ambiguities and converge on a unitary interpretation of a given scene. Our new findings also illustrate how the effectiveness of a potentially disambiguating context may critically depend on the visible surfaces it provides, and on the global relationship between objects in the scene.

Acknowledgments

This research was funded by a BBSRC research grant S20366 to J.D. & E.F., plus a UCL Bogue fellowship to E.F. J.D. holds a Royal Society Wolfson Research Merit Award. Thanks to Geoff Boynton for research support in the early experiments, and to two anonymous reviewers for constructive criticisms.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.visres.2006.07.008.

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