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Differential ambiguity reduces grouping of metastable objects

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Abstract

Two coaxial, ambiguously rotating objects tend to be perceived as corotating. Such grouping could be the consequence of bottom-up, cooperative interactions between the stimuli, or the top-down selection of object properties consistent with a model of the objects or scene. However, we find that the coupling between an ambiguous and *un*ambiguous object is sharply reduced, presenting a challenge for both explanations of grouping. We describe experiments that support the idea that top-down feedback is necessary to select and stabilize a perceptual interpretation for ambiguous figures. Reduced coupling between objects of differing ambiguity can be explained if the feedback is global and proportional to ambiguity.

Keywords: Visual grouping; Multistability; Perceptual coupling; Feedback

1. Introduction

When multiple copies of a multistable figure are viewed simultaneously, they tend to share a common interpretation and switch interpretations synchronously. Examples include the preference to see a pair of Necker cubes (Fig. 1A) as if both are viewed from above or below at the same time (Adams & Haire, 1958), or the tendency to see a field of similar triangles (Fig. 1B) as having a common pointing direction (Attneave, 1968). Similarly, a pair of ambiguously rotating lines or objects (Fig. 1C) tend to be perceived as rotating in the same direction (Eby et al., 1989; Gillam, 1972).

Theories of perceptual grouping can be classified as either stimulus-driven or model-driven. In the stimulus-driven framework, grouping is due to cooperation among neural circuits that respond to similar properties or features, such as collinearity (Alais & Blake, 1999), or common direction of motion (cf. Hock, Balz, & Eastman, 1996). Alternatively, the interpretation of a group of multistable objects may be constrained by a scene-based or object-based model imposed by the perceptual system. A scene model provides a global constraint on visual processing, such as the assumption that the scene is illuminated from above by a single light source (Enns & Rensink, 1990; Ramachandran, 1988). Object-based models interpret local stimulus information. They may be responsible for the perception of 3-D shape from line drawings (such as Necker cubes), and the predilection to perceive a hollow mask as convex (Gregory, 1980). Perceived corotation of coaxial, ambiguously rotating lines is strongest when they are arranged so that they appear to belong to a common planar surface (Gillam, 1976). This can be interpreted as an example of an object model promoting grouping of individual features.

The dichotomy between stimulus-driven and model-driven conceptions of perception corresponds to the distinction between bottom-up and top-down visual processing. The use of ambiguous figures in studies of perception is purported to be useful "for teasing out what is given upwards by cues present in the retinal image, from downwards contributions of knowledge and assumptions" (Gregory, 1997, p. 227). However some theorists have suggested that it is possible a priori constraints on perception could be learned in bottom-up associative networks (e.g. Nakayama & Shimojo, 1992). To summarize, the idea that learned models constrain perception is not controversial. But the types of models deployed by the visual system, the mechanisms by which models influence perception, and the degree to which the mechanisms are bottom-up or top-down is not well

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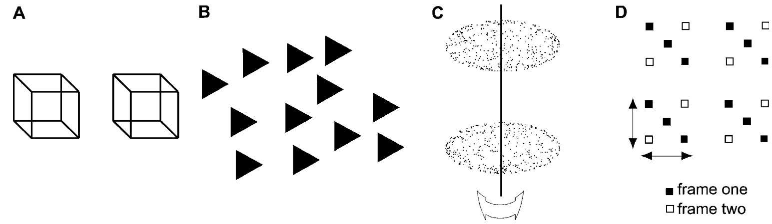

Fig. 1. Grouping of ambiguous figures. (A) Pairs of Necker cubes tend to be seen both from above or both from below at the same time, consistent with the visual experience of viewing objects from a common vantage point. (B) Attneave's triangles tend to be perceived as pointing in the same direction, or to be similar figures tilted the same way in depth (Attneave, 1968). (C) Depicted is a single frame from an animation of two kinetic dot ellipsoids rotating about collinear vertical axes. When viewing the animation, the stimuli are seen clearly as three-dimensional objects (termed the kinetic depth effect (KDE), or structure from motion (SFM)). If the objects are rendered as transparent and without perspective information, the direction of rotation of each is ambiguous. Observers tend to perceive both as rotating in the same direction at the same time (Eby, Loomis, & Solomon, 1989). (D) Dynamic dot quartets. In this two-frame animation sequence, the most common percepts are of either vertically or horizontally jumping dots. When multiple quartets are viewed simultaneously, observers overwhelmingly see the same axis of motion in all of the quartets.

understood. The present work addresses these issues by examining the basis of the perceptual coupling between ambiguously rotating objects.

Ambiguously rotating, coaxial objects (Fig. 1C) have a strong tendency to be seen rotating together. A model-driven explanation for rotational grouping suggests that the top-down influence of an object or scene model biases neuronal responses. For example, coupling between two coaxial ambiguously rotating objects is increased when they are partially hidden by an occluder so that they appear to be connected (Bonneh & Gepshtein, 2001). This might suggest that in general coaxial objects group because of an implicitly perceived physical linkage between them. Another possibility is that the visual system favors a perceptual interpretation consistent with the visual experience of flow fields generated by ego motion. Corotation is consistent with the instantaneous flow fields generated by lateral head movements when viewing coaxial objects (Dobbins, Grossmann, & Smith, 1998).

Another conjectured explanation for rotational coupling is derived from models of how the visual system resolves the depth ordering of surfaces in a structure from motion stimulus. In a model proposed by Nawrot and Blake (1991) and elaborated by Bradley, Chang, and Andersen (1998), the percept for a bistable rotating object is determined by the cooperative and competitive interactions in a cortical area such as MT (V5) that has cells selective for particular directions of motion at particular disparities. For example, the percept of an ambiguous object rotating to the left (or clockwise as viewed from above) could be the result of mutual facilitation among cells responding to leftward motion and near disparity and cells selective for rightward motion and far disparity. This cell assembly would compete with one active during the perception of rightward rotation, having cells responding to rightward motion at near disparity and leftward motion at far disparity. The competition could be implemented by inhibitory interactions between the two neural assemblies. When presented with multiple ambiguously rotating objects, crosstalk between the neural responses to each could account for rotational coupling between the two.

A prediction consistent with both model-driven and stimulus-driven hypotheses of visual processing is that perceptual coupling should remain high when an ambiguously rotating object is paired with a biased object that has an unambiguous direction of rotation. For example, if coupling is due to an implicitly perceived rotational linkage between the objects, then the biased object should specify the direction of rotation for both. Similarly, a model of perceptual coupling based on bottom-up cooperative and competitive interactions predicts that an ambiguous object should be "captured" by the biased object. The present study shows that this prediction fails for coaxial rotating objects: an ambiguous and unambiguous rotating object are effectively decoupled. This is consistent with previous findings showing that although multiple ambiguous dynamic dot quartets almost always share a common interpretation (Fig. 1D), the coupling between an ambiguous quartet and unambiguous apparent motion stimuli is much weaker (Ramachandran & Anstis, 1983, 1985).

We test several candidate explanations for the reduction in coupling between two objects with different levels of ambiguity. The results show that the reduction in coupling is not due to stimulus dissimilarity, lack of switching in the biased object, differential salience between the two objects, or due to a motion contrast effect. We present evidence that the degree of ambiguity in the two objects is the primary characteristic that correlates with the degree to which the objects are perceived to share a common sense of rotation. We describe how to account for our results by suggesting that model-based feedback is global and proportional in strength to the level of ambiguity in the objects. This leads to the prediction that when viewing a partially biased object—one which is biased to be perceived in one interpretation over the other—greater feedback is required to select the percept that has weaker evidence. Therefore when a partially biased object is perceived as rotating in the direction opposite to its bias, the degree of corotation between it and an ambiguous object should be increased. This prediction is borne out in an experiment described in Section 9.

2. Methods

In all experiments, observers viewed a computer monitor (20″ Sony Trinitron, 1280×1024 pixels at 72 frames/s) from a distance of 57 cm with their head position constrained by a chin/forehead rest. Stimuli were generated on an SGI Indigo[2] computer using custom software. Experiments using stereo defined stimuli were conducted using a frame sequential stereo display (1280×492 pixels at 60 frames/s per eye) viewed with liquid crystal shutter glasses (CrystalEyes2 from StereoGraphics Corp.), with open transmittance 30% and an open:closed transmittance ratio of 1000:1.

2.1. Experimental design

In all experiments, two stimuli (usually two rotating objects) were presented equally spaced above and below a central fixation point, with center-to-center object separation of 8°–10°. All objects were presented with vertical axes of rotation, coaxially arranged. Trial times were typically between 15 and 30 s, with an experimental session lasting between 10 and 20 min. Observers were self-paced, and encouraged to rest briefly between trials to limit fatigue. In most experiments the authors and at least three naive observers participated.

The observer's task was to maintain fixation while recording the perceived direction of rotation of both figures by pressing designated keys on the computer keyboard. Each hand was used to record the perceived direction of rotation (leftward or rightward) of one of the objects. The degree of corotation (also referred to here as "percent time coupled" and "degree of coupling") between the two objects was obtained by measuring the time both objects were reported rotating in the same direction as compared to the amount of time they were perceived rotating in opposite directions.

Most observers reported being able to pay attention to and record the directions of rotation of both objects simultaneously. In only one condition, when the task was more demanding (as discussed in Section 5), observers reported having to sometimes multiplex their attention between the two objects in order to make their responses.

Most experiments have conditions in which an ambiguous object was paired with either an unambiguous or a partially ambiguous object. In these cases, there were four counter-balanced conditions which are combined in the results. For example, in experiments pairing an ambiguous and unambiguous object, the unambiguous object appeared randomly both above and below the point of fixation, and biased rotating both rightward and leftward in different trials.

2.2. Stimulus design

Kinetic dot cubes, ellipsoids, and a shape consisting of two open hemispheres placed back-to-back (here referred to as "radar dishes") were rendered in different experiments with 160–200 randomly plotted dots, and dot sizes of either two or three pixels. We found that when viewing rotating shapes such as spheres and cylinders extrafoveally for extended periods the objects tend to undergo perceptual fading where they become difficult to apprehend as rotating objects. The shapes we used have variable 2-D profiles while rotating and are less susceptible to this type of adaptation.

Cubes (both kinetic dot and wireframe) were generated with a side length of 4°, radar dishes a radius of 2°, and ellipsoids were prolate spheroids with polar and equatorial radii of either 4° and 2° (experiment 2c) or 6.7° and 1.5° (experiment 1c). The spheroids had an equatorial axis of rotation, and were rotated 90° so that the rotational axis was vertical (Fig. 1C). Wireframe cubes were pitched 3° up or down from the plane of the screen to avoid edge alignment. All stimuli were rendered using orthographic projection. In different experiments the objects rotated at 17–30 RPM. Details of the stimuli used in individual experiments are grouped with the results of each experiment.

3. Differential ambiguity reduces grouping

In the first group of experiments, the coupling between two ambiguously rotating objects was compared to the degree of coupling between an ambiguous object and an object with an unambiguous sense of rotation. In experiments 1a through 1d the ambiguous stimuli used were: kinetic dot radar dishes, kinetic dot cubes, kinetic dot ellipsoids, and wireframe (Necker) cubes respectively. Each experiment measured the coupling between two of these ambiguous objects. In addition, in each experiment the degree of coupling was measured between an ambiguous object and an unambiguous version of the object. The unambiguous version of the kinetic dot radar dish used in experiment 1a was generated by rendering it in stereo. The unambiguous versions of the kinetic dot cubes (experiment 1b) and ellipsoids (experiment 1c) were generated by making the objects opaque, i.e., by hiding the dots on the back face. In experiment 1d, a solid shaded cube was used as the unambiguous stimulus. The cube was illuminated with a directional light source located above and to the left of the observer. (Experiment 1b contained additional conditions pairing an ambiguous object with a *partially* ambiguous object that are described in Section 8.) The number of observers was 5, 6, 5, and 4 in each experiment respectively.

Both bottom-up and top-down models of perceptual coupling predict that coupling should remain high between an ambiguous and unambiguous object. However, the results (Fig. 2A) demonstrate that coupling is high between two ambiguous objects, but that there is a marked decrease in coupling when one of the objects is given an unambiguous sense of rotation. In each experiment, the degree of coupling between two ambiguous objects is much higher than it is between an ambiguous and unambiguous object.

The levels of corotation between an ambiguous and unambiguous object in experiments 1a and 1b are indistinguishable from chance, but there are higher levels of corotation in experiments 1c and 1d. This is attributable to the fact the the objects were 45° out of phase in the first two experiments and in phase in the second two. Relative phase is known to affect grouping between ambiguously rotating stimuli and has been investigated elsewhere (Eby et al., 1989; Gillam, 1972). In all of the experiments that follow, the objects were always 45° out of phase. Another difference between these experiments is that in experiment 1a the unambiguous object was rendered in stereo, whereas in experiments 1b–1d the unambiguous object was biased by making it opaque, but without disparity information. In experiment 1a, both the front and back surfaces of the biased object were visible, presumably stimulating cells responding to motion at both near and far disparities.

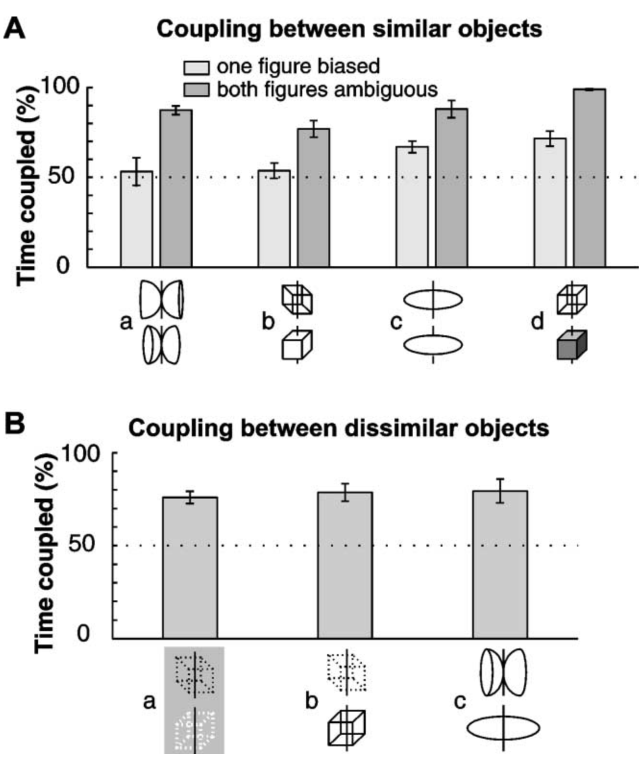

Fig. 2. (A) Differential ambiguity reduces coupling. These experiments demonstrate decreased coupling between an ambiguous and unambiguous figure. The ambiguous stimuli used in these experiments were kinetic dot radar dishes (experiment 1a), kinetic dot cubes (experiment 1b), kinetic dot ellipsoids (experiment 1c), and wireframe (Necker) cubes (experiment 1d). The unambiguous versions of these objects were a stereo rendered kinetic dot radar dish (experiment 1a), opaque versions of the ambiguous objects (experiments 1b and 1c), and a cube with faces shaded as if illuminated by a light source located above and to the left of the observer (experiment 1d). Error bars in all experiments represent the SEM. (B) Coupling between dissimilar objects. Object dissimilarity does not decrease rotational coupling between two ambiguous objects. See text for stimulus descriptions.

The results of this group of experiments, especially the fact that coupling is extinguished between a stereo rendered object and the flat (zero disparity) object, stand as a challenge to a model of coupling based solely on cooperative and competitive interactions between motion detectors. In fact, a theory of grouping based on local cooperativity might even make a prediction *counter* to these results. An unambiguous stimulus should cause a strong and unequivocal neural response resulting in a high degree of influence on the neural response to an ambiguous stimulus. Conversely, the weak neural response evoked by ambiguous stimuli should result in weak cooperativity between them, and therefore little perceptual coupling.

4. Effect of stimulus dissimilarity

Since the unambiguous version of a bistable object necessarily involves changing the stimulus in some way, e.g. by introducing binocular disparity or objects in which only the front surface is visible, we tested whether stimulus dissimilarity as such could be responsible for the reduction in perceptual coupling. According to this hypothesis, coupling could be due to the visual system interpreting ambiguous objects in the same way only when they are nearly identical.

In the second group of experiments, we tested the degree to which ambiguous objects share a common sense of rotation despite differing in either attribute definition or form. These experiments tested the coupling between opposite contrast kinetic dot cubes (experiment 2a), a wireframe (Necker) cube and a kinetic dot cube (experiment 2b), and between different kinetic dot shapes (a radar dish and an ellipsoid; experiment 2c). The objects were 45° out of phase in these experiments. There were six observers in experiments 2a and 2b, and five observers in experiment 2c.

The results for this group of experiments are shown in Fig. 2B. In all three experiments coupling remained nearly as high as it does between two identical ambiguous objects that are out of phase, such as in experiments

1a and 1b. For example, a kinetic dot defined cube paired with a Necker cube (experiment 2b) rotated together about 80% of the time, the same level as for a pair of kinetic dot cubes (experiment 1b). The radar dish and ellipsoid (experiment 2c) were perceived as coupled 80% of the time which is only about 8% less than the coupling between either an ambiguous pair of radar dishes (experiment 1a) or an ambiguous pair of in phase ellipsoids (experiment 1c). Therefore, differences in properties such as luminance contrast, shape defined by surface flow vs. edges, or even dissimilarity of form cannot account for the reduction in rotational coupling observed between an ambiguous and an unambiguous object.

5. Effect of imposed switching

During prolonged viewing of a multistable figure, an observer's perception will alternate stochastically among possible interpretations. In one model of this process, the neural representation corresponding to the active percept exhibits activity-dependent adaptation or fatigue, eventually yielding to one of the other interpretations (Hochberg, 1950). In this view, competing structures undergo alternating periods of fatigue and recovery. The unambiguous versions of the rotating figures used in the first group of experiments do not change direction of rotation within a trial. Thus it is possible that the neural representation of the unambiguous object fatigues, resulting in weaker influence on the interpretation of the ambiguous object. In addition, over the course of a trial, activity of the neural assembly corresponding to the percept of the ambiguous object may fatigue, and thus alternate, despite the influence of the unambiguous object.

To test this, we conducted a version of experiment 1a in which the unambiguous (stereo defined) version of the radar dish randomly switched its direction of rotation several times in each trial. If an unambiguous figure can influence the percept of an ambiguous figure, then the rotational reversals should reduce the degree to which the percept of the ambiguous figure fatigues in each interpretation, resulting in higher coupling. This experiment also addresses two additional hypotheses. The first is that there is a phasic neural response associated with a perceptual switch that induces rotational coupling. By imposing perceptual switches on the unambiguous object, coupling between the unambiguous object and an ambiguous object may be restored. The second is that coupling is decreased between an ambiguous and unambiguous object because the difference in bottom-up stimulus stability between the objects results in asymmetric allocation of attentional resources between the two objects. In this experiment, because the unambiguous object switches its rotation direction unpredictably, both objects must be attended to throughout every trial in order to record the reversals of each.

In this experiment, in conditions where an ambiguously rotating radar dish was paired with a radar dish rendered in stereo, the unambiguous object switched its direction of rotation randomly every 6–8 s. In conditions where both objects were ambiguous, one of the two randomly switched every 6–8 s, although this was not necessarily accompanied by a change in the perceived direction of rotation. Seven observers participated in this experiment. In a follow up experiment, we switched the unambiguous object at faster rates. In this second experiment, the unambiguous object switched every 1–3, 3–5, or 5–7 s in different trials. Four observers participated.

The results (Fig. 3A) show that random switching in the stereo-defined object does not increase rotational coupling between the ambiguous and unambiguous objects. As in the first set of experiments, the degree of

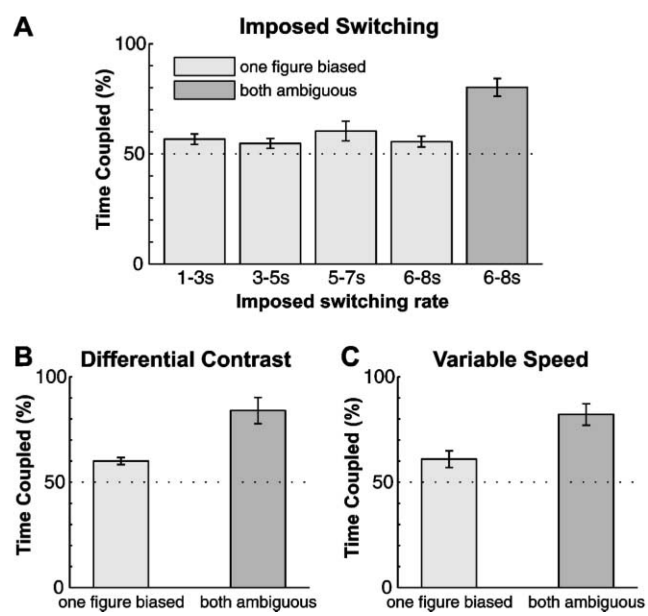

Fig. 3. (A) Effect of randomly imposed switching. The unambiguous (stereo-rounded) object in this experiment changed its direction of rotation unpredictably throughout every trial. Coupling between an ambiguous and an stereo-rounded object remains low even when the stereo-rounded object randomly switches its direction of rotation. The coupling between two ambiguous objects when one randomly switches its direction of rotation remains high. (B) Effect of differential contrast. The unambiguous object in this experiment is rendered at low contrast relative to the ambiguous object. Coupling remains as low between these objects as it is between an ambiguous and unambiguous object rendered at the same contrast levels, as in experiments 1a–1d. The results also show that coupling remains high between a pair of ambiguous objects rendered with different levels of contrast. (C) Effect of speed modulation. An attempt to increase the salience of an ambiguous object by modulating its rate of rotation fails to increase coupling between it and an unambiguous object with constant rate of rotation. Coupling between two ambiguous objects is high even when the rate of rotation of one is modulated while the other is held constant.

rotational coupling is again reduced to a near chance level, independent of switching rate. In the condition where one of two ambiguous objects randomly switched its direction of rotation every 6–8 s, coupling remained high. In addition, observers reported that the task occasionally became difficult at the fastest switching rate (1–3 s). Observers reported having to sometimes resort to a strategy where they report the direction of rotation of each object separately by alternating attention between the two. However, in the other conditions observers were able to maintain joint attention on the two objects.

These results fail to support any of the candidate explanations mentioned above for why ambiguous and unambiguous objects exhibit little or no coupling. For example, if decoupling is due to fatiguing influence from the unambiguous object, or due to the ambiguous object continuing to fatigue and alternate, then imposed reversals in the unambiguous object should have restored grouping. Similarly, neither the hypothesis that coupling is dependent on the phasic neural correlate of switching nor that an attentional asymmetry is responsible for reduced coupling is supported by the results of these experiments. If attentional demand increases with the switching rate of the unambiguous object, then a shift in attentional allocation between the objects might be expected to be manifested as a change in perceptual coupling. Instead, coupling was independent of switching rate. Nevertheless, it is not possible to completely rule out the possibility that an attentional asymmetry might alter the dynamics of rotational coupling. This is addressed in a different way in the next experiments.

6. Effect of differential salience

We evaluated other potential explanations for the reduced grouping between biased and unbiased objects. One is that ambiguous and unambiguous objects have different levels of salience to the visual system. Here we define salience as the strength of the (bottom-up) neural response to a stimulus. An ambiguous rotating dot object has balanced motion energy in opposing directions, a condition known to dramatically reduce the response of macaque MT neurons (Qian & Andersen, 1994; Snowden, Treue, Erickson, & Andersen, 1991). If coupling depends on the objects having similar salience, and an ambiguous object has reduced salience, then it should be possible to increase coupling between an ambiguous and unambiguous object by increasing the salience of the ambiguous object. Similarly, it should be possible to decrease coupling between two ambiguous objects by giving them differential salience. We tested this by measuring the degree of coupling between a low contrast unambiguous object paired with a high contrast ambiguous object. This was compared to the degree of coupling between two ambiguous objects, one with low and the other with high contrast. Low contrast objects were rendered at 25% the contrast level of high luminance objects. Stimuli were 45° out of phase kinetic-dot defined radar dishes. Unambiguous versions of the objects were rendered in stereo. Six observers participated.

The results (Fig. 3B) show no effect of differential contrast on the overall level of rotational coupling in either case. However, many MT cell responses saturate at very low contrast (Sclar, Maunsell, & Lennie, 1990). Therefore, modulating stimulus contrast may not be adequate to change the balance of neural responses to ambiguous and unambiguous stimuli, at least in area MT.

We conducted another experiment in which the goal was to increase the salience of an ambiguous object by varying its rate of rotation continuously. Continual stimulus acceleration should serve to increase the neural response to a stimulus in a cortical area such as MT (Lisberger & Movshon, 1999). In this experiment we measured the degree of coupling between an unambiguous object rotating at 20 RPM and an ambiguous object that varied its rate of rotation sinusoidally between 10 and 30 RPM with a period of 5 s. This was compared to the degree of coupling between two ambiguous objects, one rotating at 20 RPM and the other varying its rate of rotation sinusoidally as specified above. Five observers participated.

The results (Fig. 3C) show that accelerating an ambiguous object in an effort to increase its salience did not significantly increase the coupling between it and an unambiguous object. In addition, coupling remained high in this experiment between two ambiguous objects with different rotational characteristics. Neither the effort to increase object salience via object contrast nor via acceleration affected the pattern of results observed in our previous experiments.

7. Effect of motion contrast

An ambiguous kinetic dot object rotating in the midst of a large planar field of uniformly translating dots (Fig. 4A) tends to be seen as rotating in the direction opposite to the translating field (Sereno & Sereno, 1999). This finding was interpreted in terms of the subset of primate area MT (V5) neurons that have enhanced responses to motion contrast (Allman, Miezin, & McGuinness, 1985). In this view, the face of the ambiguous object moving in the opposite direction to the surrounding dots elicits the higher neural response, and thus the perception of rotation in the opposite direction.

The opaque objects used in experiments 1b–1d provide a motion stimulus in only one direction. But a transparent rotating object stimulates two populations of neurons responding to motion in opposite directions.

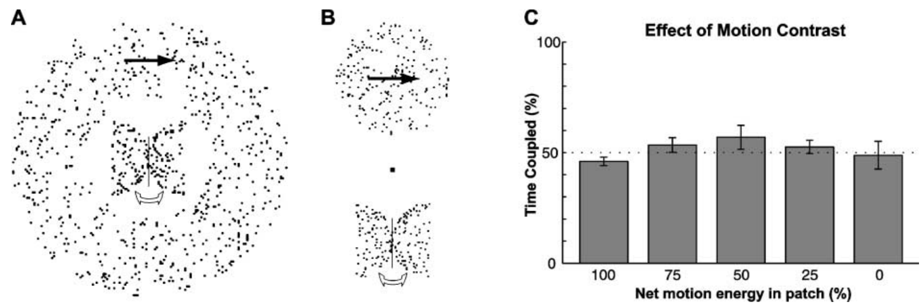

Fig. 4. (A) An ambiguously rotating kinetic dot object surrounded by a field of translating dots is strongly biased to be perceived as rotating in the direction opposite to the motion in the surround (Sereno & Sereno, 1999). (B) We tested the effect of a smaller field of translating dots on the perceived direction of rotation of an ambiguous object. Depicted is a central fixation square with a patch of translating dots above and an ambiguously rotating object below. In this experiment, the proportion of time observers perceived the ambiguous object as rotating with and against the net motion energy in the circular patch was measured. (C) Results of this experiment in which net motion energy in the patch of dots was modulated in different conditions. At 100% net motion energy, all of the dots in the patch are translating in the same direction at full contrast. At zero percent net motion energy, equal numbers of dots are translating in opposite directions, both rendered at full contrast. In the other conditions, equal numbers of dots are translating in opposite directions, but the contrast of dots in one direction is decreased relative to the dots in the other direction. There was no significant effect of motion in the patch of dots on the perceived direction of rotation of the ambiguous object.

If the two populations of neurons have antagonistic extra-classical receptive field surrounds, then the unidirectional motion energy of an opaque object located in the surround should have opposite effects on the two populations, enhancing one and suppressing the other. This could bias the ambiguous object to be perceived as rotating in the direction opposite to the unambiguous object, therefore countering the predilection to perceive corotation. We tested this hypothesis by measuring the degree to which an ambiguous object is perceived to rotate with or against the net motion energy in a circular patch of uniformly translating dots.

In this experiment, an ambiguously rotating kinetic dot radar dish appeared in different trials either above or below fixation, and a circular patch of translating dots appeared on the other side of the fixation point (Fig. 4B). The circular patch had a radius of 3° and contained dots translating horizontally at 3 deg/s. Since the purpose of the experiment was to see if the net motion energy alone in an unambiguous object biases the percept of an ambiguously rotating object, the size of the patch was chosen such that the patch covered an area just larger than that covered by the rotating dot object. In the first condition, dots translated in only one direction (either leftward or rightward), at a density of 8 dots/deg^2. In four additional conditions, the net motion energy in the patch was modulated by presenting two sets of dots translating in opposite directions, each set at a density of 8 dots/deg^2. In these conditions, dots moving in one direction were presented at full contrast, while dots moving in the other direction were rendered at either 25%, 50%, 75%, or 100% contrast. As in the other experiments, the different conditions were randomly interleaved. Six observers participated.

We found coupling to be independent of net motion energy in the patch of translating dots, being within 3%–7% of chance in all five conditions (Fig. 4C). Since there was no effect of net motion in the patch on the perceived direction of rotation of an ambiguous object, we infer that motion contrast is not the explanation for the reduced coupling between ambiguous and unambiguous objects. Note that this result does not contradict the findings of Sereno and Sereno (1999), but rather shows that much smaller patches of translating dots are not sufficient to bias the perceived direction of rotation of an ambiguous object.

8. Degree of coupling is proportional to degree of ambiguity

The first group of experiments demonstrated reduced coupling between objects having different levels of ambiguity. We also presented evidence that this does not depend on whether the objects are similar along a variety of stimulus dimensions. In this section, we show that the degree to which an ambiguous object is coupled to a second object is proportional to the degree of ambiguity of the second object.

We conducted an experiment in which the degree of ambiguity in a rotating object was modulated by varying the degree of transparency of the object. A fully ambiguous object is fully transparent and a fully unambiguous object is opaque. Intermediate degrees of ambiguity are generated by rendering the dots on the (designated) rear face at a lower contrast relative to the front face. Observers tend to perceive the brighter dots as being on the front face, thus biasing the observer to see a particular direction of rotation (first reported by Schwartz & Sperling, 1983 with rotating wireframe cubes).

This experiment paired an ambiguous kinetic dot cube with a partially ambiguous cube at transparency levels of 20%, 40%, 60%, 80%, and 100%. At a transparency of 20% the dots on the back face of the

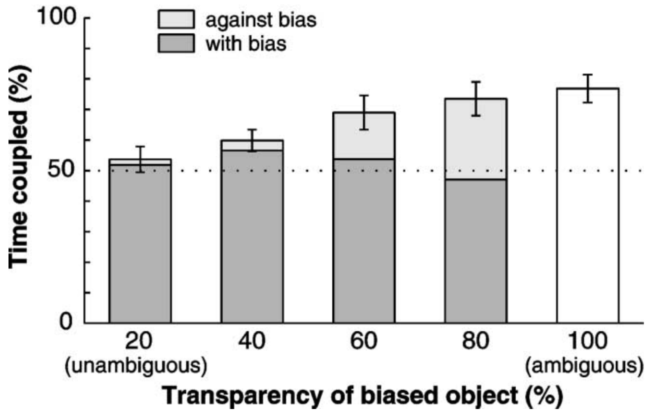

Fig. 5. Degree of coupling between an ambiguous and a partially ambiguous object. As the partially ambiguous object is made progressively more transparent (therefore more ambiguous) the degree of coupling between it and an ambiguous object increases. In addition there is an increase in the proportion of time in which the partially ambiguous object is perceived as rotating in the direction opposite of its bias. This is additional data from experiment 1b (the degree of coupling for transparency levels of 20% and 100% were shown in Fig. 1A).

object are nearly invisible, rendering the object unambiguous, while a transparency of 100% refers to a fully ambiguous figure. The results for 20% and 100% transparency are reported as experiment 1b in Fig. 2A. The results for all of the conditions in this experiment are presented in Fig. 5. The main result is that higher levels of transparency (ambiguity) result in a higher degree of coupling between the variably transparent cube and a fully ambiguous cube. The light gray portions of the stacked bar graph in Fig. 5 represent the proportion of corotation occurring when the partially ambiguous object is perceived as rotating against its bias. The more transparent the object (the weaker the directional bias), the easier it is to view it rotating in the direction opposite of its bias.

9. Cortical feedback and the grouping of ambiguous figures

This series of experiments imply that the *degree of ambiguity* of an object is the dominant property that correlates with the degree to which the object induces or is susceptible to grouping. This result is difficult to reconcile with either the stimulus-driven or model-based explanations for rotational coupling as outlined.

Our resolution to this problem begins with the suggestion that the competition between neural representations of rival percepts occurs at multiple levels in the visual hierarchy, rather than in any single area such as MT. Different levels of the hierarchy likely encode different aspects of the visual stimulus. The hypothesis we tested is that when viewing an ambiguous object, (1) greater feedback from higher to lower visual areas is necessary to select and stabilize a percept than when viewing an unambiguous object, and (2) feedback has a global influence. This suggests a feature enhancing role for cortical feedback in which neural feedback is stronger when viewing a stimulus that provides an ambiguous bottom-up signal. In this view, feedback is evoked to assist in converging on a percept when the feed-forward signals are weak due to either low stimulus salience or inhibition between neural representations such as may occur when viewing an ambiguously rotating object. Feedback acts to amplify a signal analogous to the role of feedback in an automatic gain controller.

In addition, we suppose that feedback has a global effect. This is consistent with the fact that cells higher in the visual hierarchy have larger receptive fields than cells at lower levels. Reciprocal feedback to lower level cells should affect more than just the cells with the driving stimulus in their receptive fields. Our hypothesis is that when viewing multiple ambiguous objects that have similar ambiguous properties, rotational grouping arises due to overlapping feedback from higher level visual areas enhancing properties common to both objects. For example, a cell in a higher level visual area sensitive to rightward rotation could amplify cells in earlier cortical areas responding to lower level object properties consistent with rightward rotation. If feedback has a global effect, then multiple ambiguous objects should be resolved similarly. However an unambiguous object evokes little or no feedback in order to stabilize a percept, and therefore does not affect an ambiguous object. Furthermore, the feedback that is evoked by an ambiguous object simply has no effect on an unambiguous object since it has a stable bottom-up representation.

One consequence of this idea is that stronger feedback is required to select and stabilize the percept of a *partially* transparent object as rotating in the direction opposite to its bias, because there is weaker feed-forward evidence for that percept. If this is true, then when a partially transparent object is perceived as rotating opposite to its bias, the degree of coupling with a fully ambiguous object should be increased. Fig. 6 shows the results of an experiment we conducted that tests this prediction. This experiment was identical to experiment 1b (described in Sections 3 and 8), except that the partially ambiguous object was rendered at transparency levels of 50%, 62.5%, 75%, and 87.5% in different conditions. Transparency levels less than 50% were not used because at those levels, a partially ambiguous object is rarely seen as rotating against its bias. Five observers participated in this experiment.

The results in Fig. 6 show that coupling between the partially ambiguous object and a fully ambiguous object is higher when the partially ambiguous object is perceived as rotating against its bias. In every condition,

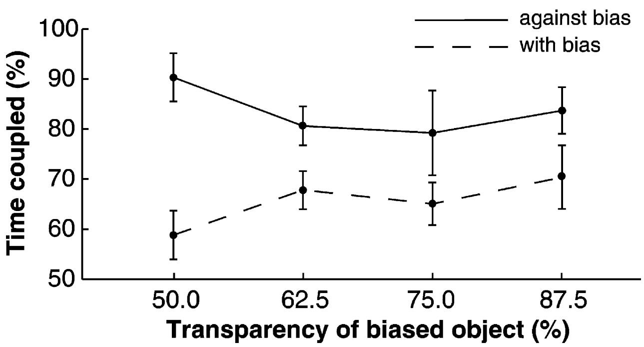

Fig. 6. Coupling conditioned on the perceived rotation direction of the biased object. In this experiment, as in the previous experiment (Fig. 5), a partially biased object is paired with a fully ambiguous object. In the analysis of this experiment we distinguish between when the partially biased object is perceived as rotating in the direction of its bias (dotted line) as compared to when it is perceived as rotating in the direction opposite to its bias (solid line). The results show a higher degree of coupling between the objects when the biased object is perceived as rotating against its bias.

coupling is above 80% when the partially biased object rotates against its bias, and below 70% when the partially biased object rotates with its bias. This disparity is greatest at the highest level of bias in this experiment (50% transparency). According to our proposal, the greatest degree of feedback is required to select and stabilize the percept of the 50% transparent object as rotating against its bias. This assertion is supported by the high degree of coupling observed in this case (~90%). Additionally, the lowest level of feedback is required to stabilize a 50% transparent object as rotating *with* its bias, as reflected in the low degree of coupling observed in this condition (less than 60%).

To summarize, Figs. 5 and 6 show data from two experiments that were identical, except that different levels of partial transparency were used. Furthermore, each figure presents a different view of the data. In Fig. 5, the degree of corotation is shown for each condition (sum of dark and light bars), as well as the proportions that the biased object was seen as rotating with and against it bias *given* corotation (dark and light portions of bars respectively). In contrast, Fig. 6 does not show the total time corotation was perceived for each condition. Instead, Fig. 6 shows the percentage of time the objects were perceived as corotating *given* that the biased object was perceived as rotating either against its bias (solid line) or with its bias (dotted line). As our hypothesis predicted, the results in Fig. 6 show that coupling is greater when a biased object is perceived to rotate against its bias.

10. Discussion

In this paper we have explored a curious asymmetry. Pairs of ambiguous objects exhibit grouping, but objects at different levels of ambiguity do not. It is unlikely that coaxial ambiguous objects group due to the perceptual system treating them as a single rigid object. Evidence for this comes from the reduction in coupling when one of the objects is disambiguated, and from the finding that coupling remains high between ambiguous objects rotating at different velocities or having unaligned rotational axes (Eby et al., 1989). However the 2-D kinetic dot and wireframe objects used in these experiments are always interpreted as 3-D objects, implicating the interpretive influence of an object model for each stimulus. Cells in the posterior parietal area of the macaque that respond preferentially to rotational stimuli were described by Sakata et al. (1994). Cells at this level of the visual hierarchy have large receptive fields and a subset of them were characterized by Sakata et al. (1994) as having a preferred direction of rotation, as preferring rotation in depth over frontoparallel rotation, and as being likely neural correlates for the perception of rotation. The neural representation of object-based models may be at least in part encoded by such cells. In addition, cells in MT that are responsive to both disparity and direction of motion have activity that is correlated with the perceived depth ordering of the surfaces of an ambiguously rotating kinetic dot object (Bradley et al., 1998). In the models of MT processing mentioned in the introduction, the network dynamics resulting from excitatory and inhibitory connections between MT cells resolve a percept for an ambiguous kinetic dot stimulus (Bradley et al., 1998; Nawrot & Blake, 1991). In these models, factors such as connection strength anisotropies and neural fatigue account for the inequalities that result in different directions of motion being resolved at different depths. Our suggestion is that feedback from an object-based representation can bias the cells responding to the the ordering of surfaces in depth. This hypothesis suggests that a higher-level representation of the rotating object exists in a higher visual area. When the bottom-up stimulus information is ambiguous, feedback from this area would serve to select the properties or features of an ambiguous object that are consistent with an activated object model. The selected properties could be represented in multiple cortical areas and include the ordering of surfaces in depth, and the sign of convexity of each surface. This hypothesis supposes that competition between rival percepts is occurring at multiple levels in the visual system, with feedback from higher to lower levels biasing lower level neural responses. Other work has demonstrated competition between high-level representations of rival stimuli presented dichoptically under stimulus conditions where lower-level rivalry processes are disrupted (Bonneh, Sagi, & Karni, 2001; Lee & Blake, 1999; Leopold & Logothetis, 1996).

Other studies have found that cell responses in V1, V2, and V3 are weakened when an area providing feedback connections to those cells, such as MT, is inactivated (Bullier, Hupé, James, & Girard, 2001; Hupé et al., 1998). This effect is most profound for low contrast stimuli, suggesting that feedback is most efficacious in shaping cell responses to weak stimuli, consistent with our hypothesis. But our hypothesis also supposes that the strength of neural feedback is *weaker* when viewing an unambiguous (high salience) object. If, instead, the strength of feedback is constant, then it is difficult to account for the results in Fig. 6 that show a difference in how an ambiguous object is perceived depending on how an accompanying partially ambiguous object is interpreted. However, a feedback signal that is weaker when a biased object is perceived to rotate with its bias *can* explain why the ambiguous object is less coupled in that case. Yet, we are unaware of neurophysiological evidence to support the idea that feedback is weaker when viewing high salience stimuli.

It is likely that feedback acts globally, or at least nonlocally, due to the large receptive field sizes of cells higher in the visual hierarchy. The idea that feedback acts nonlocally is also consistent with neuroanatomical evidence that cortical feedback connections are largely divergent and less topographically specific relative to feed-forward projections (Krubitzer & Kaas, 1989; Rockland & Knutson, 2000; Rockland, Saleem, & Tanaka, 1994; Shipp & Zeki, 1989). Furthermore, we propose a feature enhancing rather than a spatial location enhancing role for feedback. This is consistent with other studies that report a global priming effect for a particular feature when attending to that feature in another part of the visual field (Treue & Martinez-Trujillo, 1999).

According to this explanation, when viewing a pair of ambiguous objects, perceptual coupling arises as a side effect of entangled feedback elicited to determine percepts for both. We favor an explanation in which representations of objects are distributed across multiple cortical areas, and cell responses in lower-level visual areas are biased from cells higher in the visual system, over a purely feed-forward theory. This takes into account two prominent general aspects of visual processing. First, that cells higher in the visual system respond to higher-level abstractions of the visual stimulus. And second, that visual perception is strongly constrained by learned models of visual input.

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