Progress in Brain Research, Vol. 149
ISSN 0079-6123

CHAPTER 16

Interacting competitive selection in attention and binocular rivalry

Gene R. Stoner, Jude F. Mitchell, Mazyar Fallah and John H. Reynolds*

Systems Neurobiology Laboratory, The Salk Institute for Biological Studies, 10010 North Torrey Pines Road, La Jolla, CA 92037-1099, USA

Abstract: Visuomotor processing is selective — only a small subset of stimuli that impinge on the retinae reach perceptual awareness and/or elicit behavioral responses. Both binocular rivalry and attention involve visual selection, but affect perception quite differently. During rivalry, awareness alternates between different stimuli presented to the two eyes. In contrast, attending to one of the two stimuli impairs discrimination of the ignored stimulus, but without causing it to perceptually disappear. We review experiments demonstrating that, despite their phenomenological differences, attention and rivalry depend upon shared competitive selection mechanisms. These experiments, moreover, reveal stimulus selection that is surface-based and requires coordination between the different neuronal populations that respond as a surface changes its attributes (type of motion) over time. This surface-based selection, in turn biases interocular competition, favoring the eye whose image is consistent with the selected surface. The review ends with speculation about the role of the thalamus in mediating this dynamic coordination, as well as thoughts about what underlies the differences in the phenomenology of selective attention and rivalry.

Introduction

Lesion studies in monkeys have found evidence that extrastriate cortex plays a key role in visual selection. Lesions of MT (the medial temporal area) or V4 cause only relatively mild impairments in basic sensory processing such as contrast sensitivity, wavelength and brightness discrimination, form vision, orientation discrimination, motion, flicker perception, and stereopsis. In contrast, these lesions cause a profound deficit in the ability to discriminate features of a target stimulus when it is presented among salient distractors (Schiller, 1993; De Weerd et al., 1999). Lesions of Area TEO likewise cause only minor impairments in orientation discrimination, except when the discriminandum is presented with more salient distractors (De Weerd et al., 1999).

Single unit recording studies in the monkey have provided important mechanistic insights into the role of extrastriate cortex in selecting targets from among distractors. Neuronal recordings made in Areas MT and V4 have found that the response evoked by a preferred stimulus placed within the classical receptive field (CRF) is typically suppressed by the addition of a second poor stimulus within the CRF (Snowden et al., 1991; Recanzone and Wurtz, 1997). These pair responses typically correspond to an average of the responses to the preferred and poor stimuli presented individually and are consistent with competitive neuronal interactions (Reynolds and Chelazzi, 2004). Studies in V4 (Reynolds et al., 1999; Reynolds and Desimone, 2003) and MT (Recanzone and Wurtz, 1999) suggested a relationship between these competitive interactions and

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*Corresonding author. Tel.: +1-858-453-4100;
Fax: +1-858-552-8285; E-mail: reynolds@salk.edu

DOI: 10.1016/S0079-6123(05)49016-0

selective attention. These studies looked at the consequence of placing both a poor and a preferred stimulus within the CRF when attention was directed away from the CRF. Consistent with earlier studies, responses evoked by the preferred stimulus were suppressed by the addition of the poor stimulus even when the latter was excitatory when presented alone. The magnitude of this suppression was found to be determined by the neuron's selectivity for the two stimuli, such that a very poor stimulus is typically more suppressive than a stimulus that elicits an intermediate response. The relationship between the changes in firing rate associated with selective attention and these competitive interactions was studied next. It was found that directing attention to the poor stimulus magnified its suppressive effect, whereas directing attention to the preferred stimulus reduced the suppressive effect of the ignored poor stimulus. These pair responses approximate a weighted average of the responses to the stimuli presented individually. These patterns of neuronal responses are consistent with a model of selective attention in which feedback signals from areas such as the frontal eye fields (Moore and Fallah, 2001; Moore and Armstrong, 2003) bias competitive circuitry intrinsic to the visual cortex.

If different stimuli are presented to the two eyes, *binocular rivalry* usually results — only one of the two stimuli is perceived at any given time. Binocular rivalry involves visual selection of a qualitatively different sort than that observed during selective attention in which attending to one of the two stimuli does not render the unattended stimulus invisible. Despite this important phenomenological difference, there is reason to think that attention and rivalry may depend on common stimulus selection mechanisms (Lumer et al., 1998; Leopold and Logothetis, 1999), an idea that has been debated as far back as the late 19th century (James, 1890; Helmholtz, 1909). There are neurophysiological data supporting this view. Single-unit recording studies of binocular rivalry suggest that neuronal suppression becomes more strongly correlated with perceptual suppression as one moves from V1 to IT (Sheinberg and Logothetis, 1997; Logothetis, 1998). A similar trend can be seen in attention, where attended stimuli gain increased influence over neuronal responses as one moves from early to later stages of processing (Motter, 1993; Chelazzi et al., 1993; Reynolds et al., 1999; Sheinberg and Logothetis, 2001). Thus, selection during attention, as well as during rivalry, appears to depend on competitive interactions occurring at multiple stages with progressively greater accumulated effect as one ascends the cortical hierarchy. This neurophysiological commonality suggests a potential relationship between selective attention and binocular rivalry.

What is selected: features, locations, eyes, or surfaces?

Another connection between binocular rivalry and selective attention is that the question of exactly what is selected has been the subject of debate in both domains. The attention studies discussed above used spatially separated stimuli that were defined by different features (e.g., upward vs. downward motion). Therefore, it is not possible to say whether the competitive mechanisms examined mediate selection of a spatial location, a specific feature, or the object that occupies the attended location. However, while it is well established in the attention literature that spatial locations (Posner, 1980; Treisman and Gelade, 1980) and single features (Saenz et al., 2002) can be selected for preferential processing, it is now recognized that an object or surface can also be selected (Duncan, 1984; He and Nakayama, 1995). For example, Blaser et al. (2000) found that observers were able to track the color, orientation or spatial frequency of one grating when another grating was spatially superimposed. They found that tracking two features of one grating was no more difficult than tracking one feature, suggesting that attention selects the whole stimulus. Tracking two similar features of different gratings was markedly more difficult, suggesting that selecting one stimulus impaired selection of the other stimulus. In the rivalry literature, the debate over what is selected has centered on whether rivalry reflects competition between stimulus representations (stimulus-based rivalry), interocular competition (eye-based rivalry), or some combination of the two (Blake and Logothetis, 2002). The latter view, consistent with the neurophysiological findings discussed above, implies that interocular competition within area V1 and feature-based competition within extrastriate cortex both contribute to binocular rivalry. This view remains controversial, however, as functional imaging studies suggest that inter-ocular competition within area V1 may be sufficient to account for the perceptual suppression occurring during binocular rivalry (Tong and Engel, 2001, Polonsky et al., 2000).

Recent psychophysical studies have shown that attention can select surfaces or objects (Valdes-Sosa et al., 2000; Pinilla et al., 2001; Mitchell et al., 2003; Reynolds et al., 2003). These studies have ruled out spatial selection by using spatially superimposed dot fields and have ruled out attention to a single feature by having the dot fields abruptly change from rotation to translation in a random direction. This approach has been adapted to determine whether binocular rivalry and attention shared a surface-based selection mechanism (Mitchell et al., 2004). This paradigm is illustrated in Fig. 1. Observers viewed rigid patterns of dots presented to both eyes at the start of each trial. The dot patterns rotated in opposite directions around the fixation point, yielding a percept of two superimposed transparent surfaces. After a period of dual rotation, one of the surfaces underwent a brief translation in one of eight directions, and the observer discriminated its direction of motion. This brief translation has previously been found to have a cueing effect such that the translated surface has a temporary perceptual advantage (Valdes-Sosa et al., 2000; Pinilla et al., 2001; Mitchell et al., 2003; Reynolds et al., 2003). Accordingly, the surface that underwent translation is referred to as the *cued surface*. Following this translation, the cued surface was removed from one eye and the uncued surface was removed from the other eye. This dichoptic condition yielded a rivalrous percept. To determine whether the cued surface was dominant during rivalry, observers were asked to report whether one surface was clearly dominant at the end of dichoptic presentation, and if so, which surface. By varying the duration of dichoptic presentation from trial to trial, the time course of dominance from 0–1850 ms was traced.

As illustrated in Fig. 2A, for a brief time after the switch to dichoptic presentation, neither surface clearly dominated, consistent with previous measures of the time for perceptual dominance to develop during rivalry (Wolfe, 1986; de Belsunce and Sireteanu, 1991; Leonards and Sireteanu, 1993). However, after 300 ms of dichoptic viewing, rivalry was perceived on 70% of the trials, and the cued surface was usually dominant. The translation that cued attention was presented equally to both eyes. Nonetheless, the translating surface was dominant, irrespective of whether it appeared in the right or left eye during subsequent dichoptic viewing. Thus, the dominance of the cued surface did not result directly from a bias of interocular competition.

Rather, it appears as though the visual system selected the translating surface and suppressed the other surface. If so, observers should be impaired in making judgments of the suppressed surface. Observers had to perform a double translation task, in which they reported the direction of a second translation that occurred during rivalry. As before, 150 ms after the first translation, one surface from each eye was deleted, but instead of asking observers to report which surface was then dominant, they were asked to report the direction of the second translation. As illustrated in Fig. 2B, observers were impaired in judging the uncued surface during rivalry. This impairment was weak but significant (two-tailed *t*-test, $p < 0.05$) immediately after the onset of dichoptic viewing, agreeing with the relatively weak perceptual dominance found following the shortest period of dichoptic viewing (Fig. 2A). Observers were strongly impaired at judging translations of the uncued surface at longer dichoptic presentation times, when they had reported that the cued surface was dominant. Note that this impairment was surface- and not merely feature-dependent: the identical translation (e.g., an upward translation) was either reported accurately or not, depending only on which surface had previously translated. Thus, a surface-based cue during binocular viewing determined which surface would be judged accurately during subsequent rivalry, and this cueing effect had a timecourse that matched that of perceptual dominance.

A simple modification of the stimulus enabled the study to directly compare the impairments observed during attention and rivalry. In the double translation task, trials in which the stimuli were perceived as superimposed transparent surfaces were interleaved throughout the trial. On half of these transparency trials, both surfaces were presented to both eyes

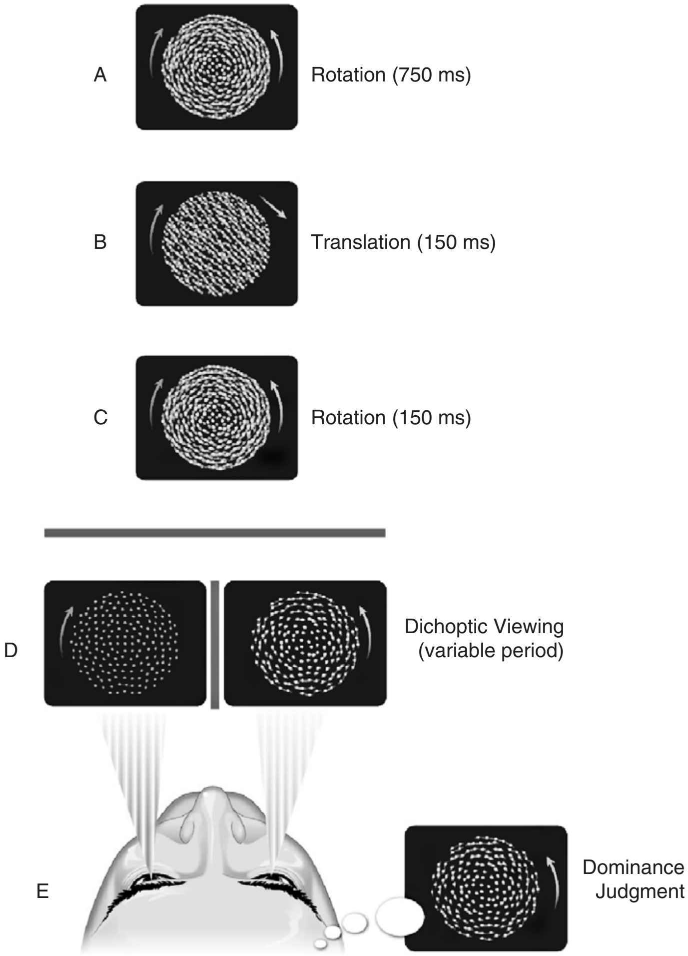

Fig. 1. Task. Panels are arranged from top to bottom according to the sequence of events in each trial. (A) Two sets of dots rotated in opposite directions around a common point, yielding a percept of superimposed transparent surfaces viewed through an aperture. Both sets of dots were identical in color. They differ here in gray level for purposes of illustration. (B) One of the surfaces translated for 150 ms in one of eight directions, while the other surface continued to rotate. Subjects reported the direction of translation. (C) Both surfaces resumed rotating for 150 ms. (D) One surface was removed from each eye, resulting in rivalry. Subjects judged which surface was dominant at the end of this variable-length period of rivalrous viewing. (E) Observers usually perceived the previously translated surface as dominant. (Reproduced courtesy of Nature.)

throughout the trial, a condition that would be referred to as *binocular transparency*. On the other half of the transparency trials, both surfaces were deleted from one eye 150 ms after the first translation. This *monocular transparency* condition controlled for the momentary disruption caused by deleting surfaces in the switch from normal binocular viewing to rivalrous viewing, but without actually inducing rivalry, as there was no competing stimulus in the other eye. Despite this transient event, when switching to monocular transparency there were no significant differences in observers' performance on monocular and binocular transparency trials. Therefore, we focus on monocular transparency, as it provides a more direct comparison to rivalry.

As illustrated in Fig. 2C observers were impaired in judging the uncued surface during monocular transparency, but with a different timecourse than

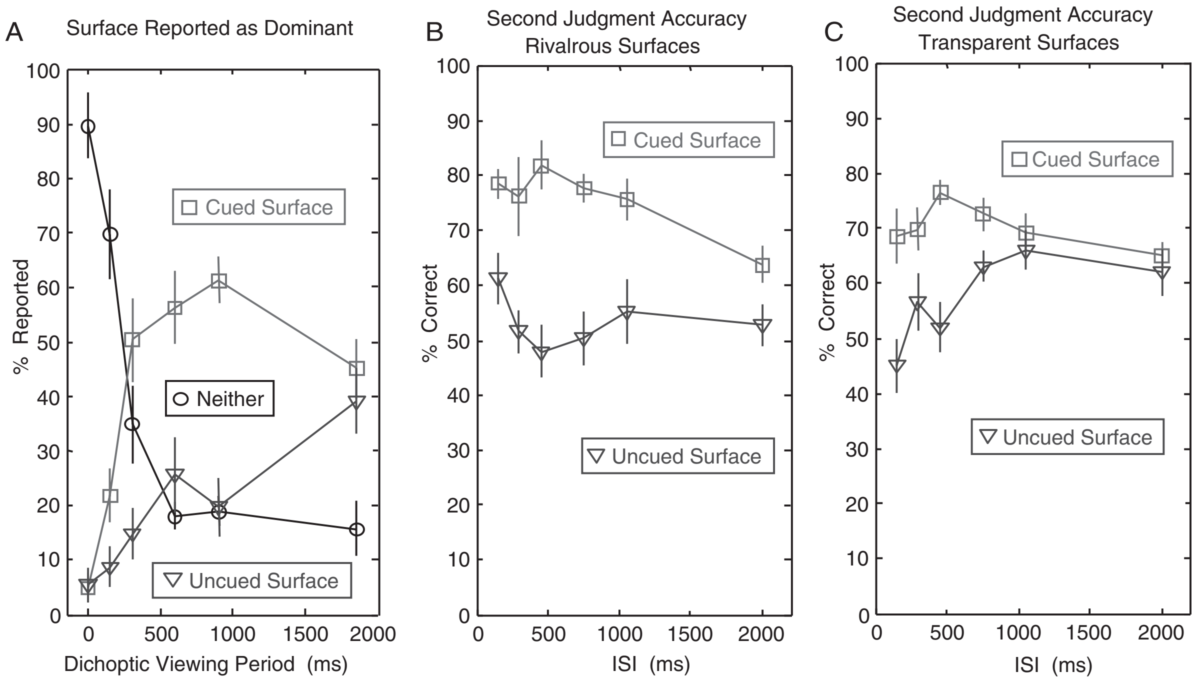

Fig. 2. (A) Seven observers reported whether either surface was dominant at the end of dichoptic presentation, and if so, which surface had been dominant. The mean percentage of trials on which the cued or uncued surface was reported to be dominant is indicated by the square symbols and triangle symbols, respectively. The percentage of trials on which neither surface was clearly dominant is indicated by circle symbols. (B) Mean accuracy in reporting the direction of the second translation averaged across trials in which the surfaces were presented dichoptically. (C) Mean accuracy in reporting the direction of the second translation when both surfaces were presented to one eye, and thus appeared as transparent. Lines in B and C indicate whether the cued (square symbols) or uncued surface (triangles) translated second. The interstimulus interval (ISI) is the delay between the end of the first translation and start of the second translation (ISI = dichoptic viewing period +150 ms). Error bars indicate standard errors of the mean (SEM) across subjects. (Reproduced courtesy of Nature.)

in rivalry. The impairment was strongest 150 ms after the first translation and disappeared within 1000 ms. In contrast, the peak impairment in rivalry was delayed until 450 ms after the first translation, and the impairment persisted even for the longest period tested. This difference in the size of the impairment and its timecourse was highly statistically significant.

Discussion

These experiments provide the first evidence that surface-based attention influences selection during binocular rivalry. Presenting the first translation binocularly ensures that dominance could not result directly from biasing interocular competition. Rather, the translation during transparency caused a surface to be selected and to emerge as dominant during subsequent dichoptic viewing. This selection was not feature based — the translation cue impaired direction-of-motion judgments of the non-dominant surface during rivalry but not of the dominant surface. This surface-specific impairment during rivalry followed the same timecourse as that seen for the dominance judgments. These results thus extend the notion of stimulus-based rivalry (Diaz-Caneja, 1928; Whittle et al., 1968; Kulikowski, 1992; Kovacs et al., 1996; Logothetis et al., 1996; Alais and Blake, 1998; Alais and Blake, 1999; Lee and Blake, 1999) to include surface-based rivalry.

The fact that a surface-based cue presented during binocular viewing determines the surface that will be judged accurately during both rivalry and transparent surface perception supports the view that, despite their obvious phenomenological differences, rivalry and attention rely on a partially overlapping set of competitive mechanisms. Evidence for stimulus-based competition has been used to argue that binocular rivalry falls within the general class of multistable percepts that also includes the Necker cube, the face–vase illusion, bistable cylinders and other stimuli that alternate between competing interpretations in the absence of inter-ocular differences (Logothetis, 1998; Dodd et al., 2001). The present results thus raise the intriguing possibility that the selection of ambiguous or conflicting stimulus interpretations (as with bistable percepts) and the selection of one of several possibly relevant stimuli (during selective attention) reflect the operation of an overlapping set of competitive mechanisms.

How do competitive mechanisms interact?

Neurons selective for rotation, translation, and eye-of-origin reside, for the most part, in different cortical areas. Thus, although neurons selective for direction of translation are found in various cortical areas, there are several lines of evidence that demonstrate the importance of area MT in the recovery of direction of object motion especially, as reviewed above, in the presence of multiple stimuli. Neurons selective for direction of rotation conversely are found in MST but rarely in MT (e.g., Lagae et al., 1994). Neurons with strong ocular biases are found exclusively in area V1. Given these cortical specializations, the continued dominance of a surface as it sequentially activates rotation-selective neurons and translation-selective neurons would seem to require that different neuronal populations in areas MT and MST communicate the identity of the dominant surface to one another as first one and then another become selectively activated. Likewise, the continued dominance of the cued surface after the transition to rivalrous viewing suggests that the motions encoded in areas MST and MT are somehow linked, in a surface-specific manner, with V1 neurons selective for eye-of-origin. Neither the mechanisms nor the neuronal pathways that subserve this linkage are known.

Possible role of the thalamus

Direct corticocortical connections offer one possibility (Felleman and Van Essen, 1991) but the cortico-pulvinar-cortical pathways (Sherman and Guillery, 2003) offer an alternative. There are several intriguing lines of evidence that suggest a possible role for the pulvinar nucleus of the thalamus in surface based selection. First, pulvinar lesions in humans have been found to result in an inability to correctly conjoin features (Ward et al., 2002). Second, lesions of the pulvinar also result in deficits in selective attention (e.g., Danziger et al., 2004; Michael and Desmedt, 2004). Third, there is evidence that the diffusely projecting neurons of the thalamus may be involved in synchronizing neuronal activity across different cortical areas (Jones, 2001, 2002). The functional importance of synchrony is controversial but has been implicated in both selective attention (Fries et al., 2001) and feature binding (e.g., Castelo-Branco et al., 2000, Thiele and Stoner, 2003). Fourth, the different firing modes of thalamic relay cells (burst and tonic) may underlie selective processing of stimuli, with bursting associated with shifts of attention and tonic firing associated with continued scrutiny (Sherman and Guillery, 2003). These various lines of evidence, taken together, suggest the (admittedly highly speculative) idea that the thalamus may play a critical role in surface-based selection.

What accounts for differing phenomenology of attention and rivalry?

The double translation experiments isolated the contribution of neurons that mediate inter-ocular competition. Transparency and dichoptic viewing trials began identically, with one of the two surfaces cued by a sudden translation. Stimulus conditions were identical during cueing, so the same neurons logically must have been engaged, regardless of whether transparent or rivalrous viewing ensued. From this, it is surmised that the same object-based mechanisms initiated selection for both transparency and rivalry trials. However, after the cueing phase, the sole difference between the rivalry and monocular transparency conditions was that the two deleted stimuli were removed from different eyes in one condition and from a single eye in the other. Thus, whereas dominance during rivalry and transparency must have been triggered by the same object-based mechanisms, the differences in the timecourses of selection and phenomenology can only be due to neurons with eye-of-origin information.

As neurons with strong selectivity for eye-of-origin are found in V1, these differences plausibly are due to the involvement of V1. One way of reconciling the evidence that binocular rivalry depends upon interocular competition with the evidence implying competition at multiple interacting stages is to assume that interocular competition within V1 underlies the complete perceptual suppression associated with binocular rivalry, but that which eye's input is dominant can be influenced by input from competitive mechanisms within extrastriate areas. If area V1 does indeed play a special role in perceptual suppression during rivalry, it may be because of its unique placement in the cortical hierarchy or perhaps because interocular competition is stronger than feature- and surface-based competition and hence leads to a winner-take-all selection.

Acknowledgments

The authors acknowledge funding provided by NEI grant 5 R01 EY012872-06 (GRS), PHS/33201A/T32MH2002 (JFM), NEI grant 1R01EY13802 (MF), and a grant from The McKnight Endowment Fund for Neuroscience (JHR).

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