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Research Article

Voluntary Action Influences Visual Competition

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ABSTRACT—*Converging lines of evidence point to a strong link between action and perception. In this study, we show that this linkage plays a role in controlling the dynamics of binocular rivalry, in which two stimuli compete for perceptual awareness. Observers dichoptically viewed two dynamic rival stimuli while moving a computer mouse with one hand. When the motion of one rival stimulus was consistent with observers' own hand movements, dominance durations of that stimulus were extended and, remarkably, suppression durations of that stimulus were abbreviated. Additional measurements revealed that this change in rivalry dynamics was not attributable to observers' knowledge about the condition under test. Thus, self-generated actions can influence the resolution of perceptual conflict, even when the object being controlled falls outside of visual awareness.*

The idea that perception and action are tightly linked is an old one within psychology, dating back to the 19th century, when James (1891) proposed that movements are coded in terms of their anticipated sensory consequences. In the 20th century, Gibson (1979) effectively championed the idea that perception and action are inextricably linked, and his writings have been influential in shaping work on a number of problems, including optic flow and the perception of causality. In recent years, new evidence has shown that a person's actions—or even intended actions—can influence what that person sees (Kunde, 2004; Prinz & Hommel, 2002; Thornton & Hayes, 2004; Wohlschläger, 2000). For example, in the domain of biological motion, an observer's ability to discriminate the gait speed of an animated point-light walker depends on whether or not the observer is walking him- or herself (Jacobs & Shiffrar, 2005).

In the present study, we asked whether the linkage between action and perception extends to stimulus conditions involving visual conflict. Specifically, we determined whether motor actions or motor intentions can influence the dynamics of binocular rivalry, the unpredictable fluctuation in visual perception that occurs when the two eyes view radically different stimuli (Blake & Logothetis, 2002). During binocular rivalry, one of two stimuli achieves exclusive dominance for several seconds at a time, while the other stimulus is suppressed from visual awareness. It is well established that stimulus variables such as contrast, complexity, and motion can influence rivalry dynamics (Blake, 2001). But can the predominance of a visual event viewed by one eye also be influenced by an observer's active production of that event? An answer to this question is timely and important for two reasons.

First, an answer to this question would bear importantly on current theorizing about the neural bases of binocular rivalry (Tong, Meng, & Blake, 2006). According to one class of models, binocular rivalry arises from dynamic, competitive interactions between neural elements that exhibit response adaptation over time (Laing & Chow, 2002; Wilson, 2003). As currently construed, these models treat rivalry as an encapsulated process uninfluenced by motor intentions or control. These models predict, in other words, that rivalry dynamics should be immune to action or intentions. Other, contrasting models treat rivalry as the outcome of competition between object-based representations, with alternations in perceptual dominance arising from the operation of "active, programmed events initiated by brain areas that integrate sensory and non-sensory information" (Leopold & Logothetis, 1999, p. 254). Because visual selection depends importantly on planning and execution of behavioral actions in these models, they suggest that the dynamics of binocular rivalry could be significantly influenced by an observer's control of a rival stimulus.

Second, evidence for action's influence on rivalry could have even broader implications for understanding the relation between executive control and consciousness. Some researchers believe that self-controlled actions are enabled by the same neural structures that embody consciousness (Dehaene & Naccache, 2001). According to this view, an observer's motor control over a rival stimulus should have no influence on the

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fate of that stimulus when it is suppressed, because the observer's actions affecting that stimulus have been uncoupled from conscious awareness. Other researchers, however, believe that aspects of control can be monitored outside of awareness, with the consequences of that monitoring affecting the resolution of behavioral conflict (Botvinick, Braver, Barch, Carter, & Cohen, 2001). According to this view, the fate of a suppressed stimulus could indeed be influenced by an observer's actions controlling that stimulus even though it falls outside of conscious awareness.

We cannot specify a priori exactly how action would influence rivalry dynamics, but the findings of earlier rivalry experiments suggest several possibilities. Active control of a rival stimulus could produce an increase in the average duration of dominance of the controlled stimulus or a decrease in the average duration of suppression of that stimulus; either result would allow for longer perception of the controlled stimulus. Indeed, these kinds of changes in rivalry dynamics have been observed in other contexts in which stimulus strength (e.g., Bossink, Stalmeier, & deWeert, 1993) or the global context (e.g., Sobel & Blake, 2002) has been manipulated during rivalry.

It should be noted that none of the many studies of rivalry performed over the years have used a procedure that would assess action's influence on rivalry. In all of those experiments, people have never been engaged in voluntary activity relevant to either rival stimulus, other than to push a button indicating which one was dominant. The experiment reported here was unique in using rivalry as a means for studying the relation between awareness and control, a problem of central importance in contemporary cognitive neuroscience (Mayr, 2004).

METHOD

Observers viewed rivalry between a flickering grating and a sphere whose rotation, on some trials, was under their control. During an initial training phase, participants learned to move a computer mouse in a prescribed manner. During the test phase, they continuously performed these trained mouse movements and tracked dominance and suppression durations of the grating and the rotating sphere; on some trials, they controlled the sphere, and on other trials, they did not. During the discrimination phase, observers judged whether a briefly presented, rotating sphere was being controlled by their concomitant hand movements. This phase allowed us to assess sensitivity to self-produced movement.

Apparatus

Stimuli were displayed on a CRT monitor (1280 × 1024 resolution, 60-Hz frame rate) controlled by a Macintosh G4 computer and were viewed through a custom-built mirror stereoscope with the head stabilized by a chin-and-head rest.

Observers

Five observers participated in the experiments. Two observers were authors of this article, and the remaining 3 were naive to the purpose of the study. All had normal or corrected-to-normal acuity and good stereopsis. All observers gave signed consent after being informed of the nature of the tasks.

Stimuli and Procedures

Training Phase

During the training phase, observers practiced making smooth hand movements with the computer mouse; these movements would later be produced in the test phase, when mouse movements would cause smooth, continuous rotation of the sphere. Observers viewed two vertical bars displayed within a rectangle (1° × 6.67°) in the center of the monitor (see Fig. 1a). One bar (1° × 0.67°), shown in red in Figure 1a, oscillated horizontally with a sinusoidal speed profile of 0.25 Hz and served as a reference; the other bar, shown in green in Figure 1a, was the target bar (1° × 0.05°), and its motion followed the observer's mouse movements. The observer's task was to move the mouse laterally back and forth to achieve and maintain alignment of the target with the reference bar during each 30-s trial. The computer monitored the position of the mouse (sample rate = 60 Hz), and at the end of each trial, the computer calculated an error score, which was proportional to the deviation between the position of the median line of the reference bar and the position of the target bar. Tracking performance was deemed successful for a given trial when the average deviation between the target and reference bars over the 30-s period was less than 2.8% of the width of the reference bar (a deviation corresponding to 1.1 arc min). Figure 1b shows an example of a "successful" record of mouse movements produced by 1 observer during a 30-s training sequence. When an observer had completed 10 successful trials, the training phase was terminated, and the mouse movements for the last trial were recorded for use in subsequent phases of the experiment.

Test Phase

The test stimuli were dissimilar images (1.33°) generated on the left and right halves of the monitor and presented against a uniform gray background (Fig. 2a). The luminance level of the gray background was 41.5 cd/m^2. The two images included carefully designed fusion contours (2° × 2°) surrounding the rival targets to promote stable eye alignment. One rival target was an animation portraying dynamic 2-D projections of a rotating sphere, and the other rival target was a radial grating. Over trials, the eyes viewing the sphere and the grating were counterbalanced.

The sphere was a cinematogram whose successive animation frames constituted the 2-D projection of a 3-D object: a rotating, transparent sphere defined solely by dots (Gilroy & Blake, 2004). These random-dot cinematograms of a structure-from-

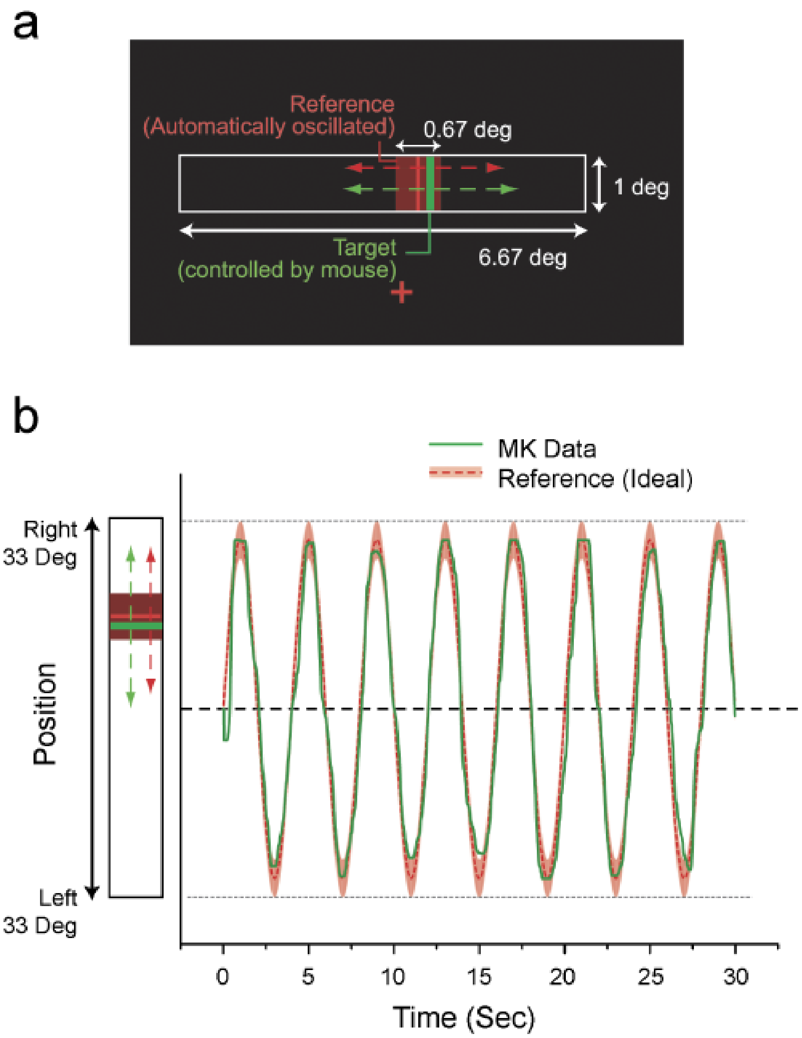

Fig. 1. Stimuli (a) and example of results (b) from the training phase. Observers controlled the green target bar with a handheld mouse and tried to align it with the middle of the moving, red reference bar (the middle was demarcated by a thin, bright, red line). In (a), the median line on the reference bar shows the exact position of the target bar in the ideal sinusoidal movement. In (b), the red line shows the ideal sinusoidal movement profile, as indicated by the median line in the reference bar, and the red area shows the width of the reference bar. The green line shows the profile produced by observer M.K. in his final successful trial.

motion sphere were created by the orthogonal projection of a mathematically defined, rotating 3-D sphere. Each frame of the cinematogram consisted of 150 (5 × 5 arc min) white dots representing random points on the surface of a 3-D sphere with a diameter of 1.33°. Ambiguity about direction of rotation was removed by not displaying dots associated with the far side of the sphere. The luminance contrast between the dots and the background was fixed to 0.65. All the dots' positions were updated every 16.6 ms, creating the perception of smooth, continuous motion of a sphere in 3-D space. The speed and direction of rotation were controlled by observer-controlled movements of the computer mouse or by records of previously produced mouse movements. In the former case, the motion sequences were sampled at 60 Hz and stored on disc so that we could repeat the exact same sequences of rotations on later trials. When an observer moved the mouse back and forth and, thus, moved the dots defining the sphere leftward and rightward, the observer's sense of control over the sphere's rotation was immediate and vivid.

The grating consisted of a central disk surrounded by five annuli, each of which consisted of alternating light and dark sections. The contrast of each annulus reversed every 167 ms to generate a flickering pattern (6 Hz). The luminance contrast of the grating was customized for each observer to promote unambiguous dominance and suppression phases of the sphere and grating, with minimum instances of mixed dominance.

The test phase consisted of 160 trials distributed over four sessions of 40 trials each. Two of the four sessions consisted of sphere-dominant trials (together constituting the sphere-dominant condition), and the other two sessions consisted of sphere-

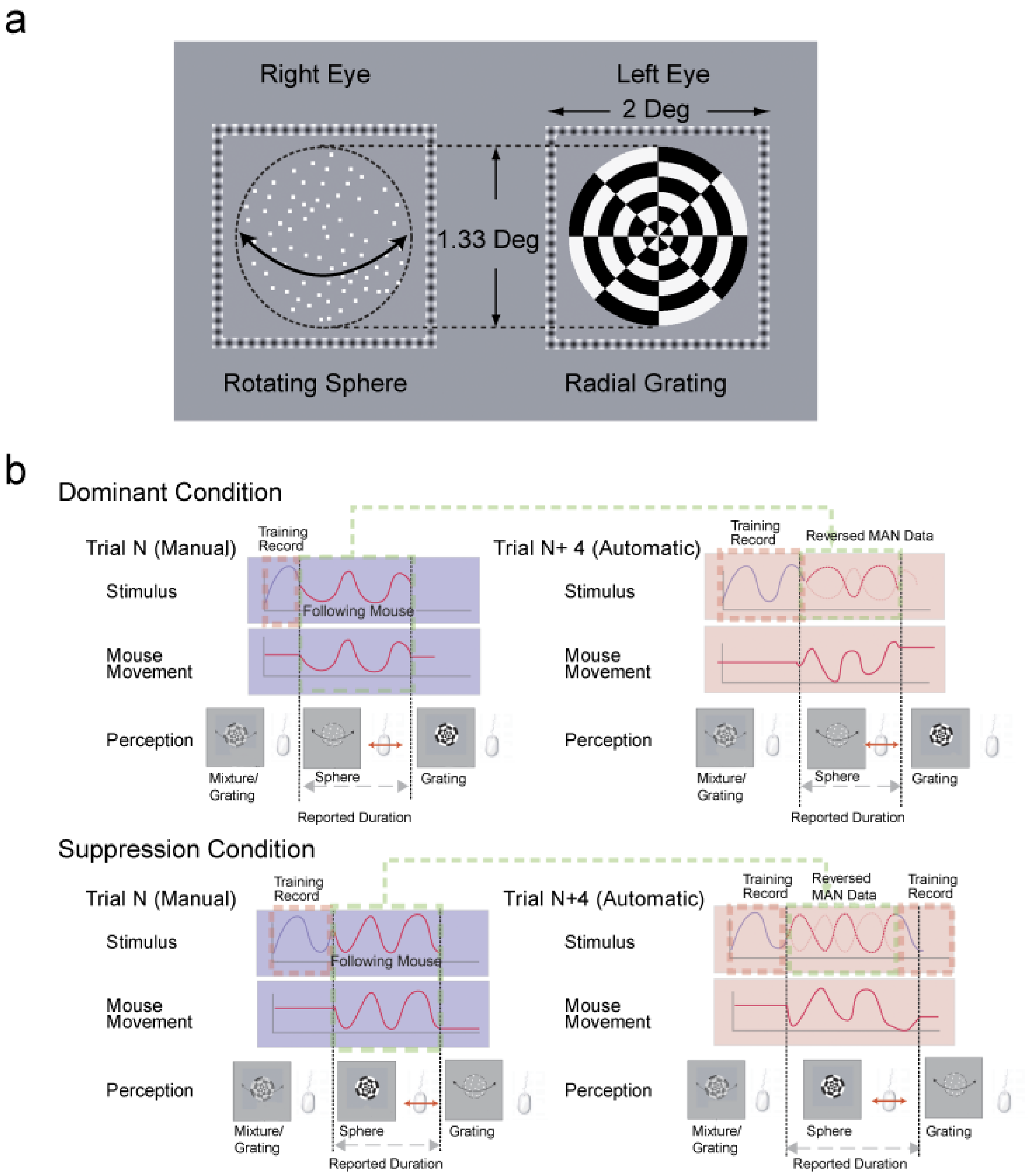

Fig. 2. Schematic depiction of the rivalry stimuli (a) and diagrams illustrating the four kinds of trials (b). In the experiment, the reversed configuration of the stimuli, with the sphere exposed to the left eye and the grating exposed to the right eye, was also used. In (b), each diagram shows the dots' movement, the observer's hand movement, and the observer's perception of the stimuli, as a function of time. The diagrams in the upper row illustrate the sphere-dominant condition, and the diagrams in the lower row illustrate the sphere-suppressed condition; manual (MAN) trials are shown on the left, and the corresponding automatic trials are shown on the right. The dashed orange outlines indicate the period during which sphere rotation followed the rotation in the training phase, and the green arrows show the correspondence between the sphere-rotation profiles in manual and automatic trials (see the text).

suppressed trials (sphere-suppressed condition). In the sphere-dominant trials, observers were instructed to initiate hand movements when the sphere achieved exclusive visibility, with no hint of the grating's presence, and to continue moving the mouse until the sphere was no longer exclusively visible. Thus, the duration of hand movements in each trial provided a measure of the duration of sphere dominance for that trial. In the sphere-suppressed trials, observers were told to begin hand movements when the grating became exclusively visible and to continue moving the mouse until that perceptual state changed. These trials provided a measure of the duration of suppression of the sphere.

Before each trial in the test phase, reference contours were presented to each eye to allow for fusion of the two eyes' views. The observer pressed any key to begin a trial, at which point the rival stimuli increased in luminance contrast linearly over 0.5 s to reach the values appropriate for that observer. At the onset of each trial, the motion vectors of the dots defining the sphere were controlled by a record of the mouse movements associated with the last trial of the training phase; these records were selected for each observer from his or her own training-phase data. Once the designated rival state was achieved (sphere or grating dominant), the observer began moving the mouse laterally in the manner learned during the training phase. When the designated rivalry state ended, the observer ceased mouse movements, and the trial ended. Observers were asked to move the mouse in the same manner that they learned during the training phase.

On some trials (*manual*), the concurrent mouse movements controlled the motion vectors of the dots defining the sphere; in addition, these mouse movements were recorded and stored. On other trials (*automatic*), the dots were defined by motion vectors recorded from previous manual trials, not by the observer's concurrent hand movements on that trial. In a given session, manual and automatic trials were presented in five blocks, each consisting of 4 manual trials followed by 4 automatic trials. The recorded mouse-movement data in each manual trial (trial n) within a block were reversed in direction and used in the corresponding automatic trial within that block (trial $n + 4$; see Fig. 2b). Reversing the hand-movement profiles ensured that the on-line hand movements differed from the dots' motion during automatic trials. As soon as the observer began hand movements in an automatic trial, the sphere's motion was controlled by previous manual data that were reversed in direction. If the observer's hand movements exceeded the duration of the movement record being used on that trial, the movements from the observer's last training trial were then utilized for the remainder of that trial. Transitions from one control source of dot motion (e.g., previous manual trial) to another (e.g., training record) were implemented smoothly to avoid abrupt transients that could perturb rivalry. On a small fraction of the trials (3% of the total, evenly distributed between the automatic and manual conditions), observers inadvertently produced brief mouse movements that registered dominance durations lasting only a few hundred milliseconds. Those values were discarded from data analysis.

Discrimination Phase

In the discrimination phase, we investigated observers' ability to distinguish between the manual and automatic trials. The procedure was basically the same as in the dominance condition of the test phase (i.e., observers were told to initiate mouse movements when the sphere was dominant and to discontinue movements once the sphere was completely suppressed). However, in some trials assigned to the manual condition, the direction of motion associated with hand movements was reversed to discourage observers from basing their judgments solely on the motion direction of the sphere, because it was always reversed in the automatic condition. Also, the order of manual and automatic trials was randomized, with the exception of the first 4 trials, which were always manual (these were not included in the data analysis, but were necessary to generate records to be used for successive automatic trials). Observers performed 40 manual trials and 40 automatic trials. Trials terminated automatically 3 or 5 s after observers began moving the mouse (the two motion durations were presented in separate blocks). At the end of a trial, observers pressed one of two keys to indicate whether or not they felt that their hand movements had controlled the motion of the sphere on that trial. They were told to guess if they were completely uncertain and to distribute their guesses equally between the two alternatives.

RESULTS

Rivalry Dynamics

Average durations of mouse movements for the manual and automatic conditions are plotted in Figure 3a; the graph on the left summarizes results for trials on which mouse movements were initiated when the sphere was dominant (sphere dominant), and the graph on the right summarizes results for trials on which mouse movements were initiated when the grating was dominant (sphere suppressed). First, notice the individual differences in average dominance durations, an outcome entirely consistent with previous results showing significant variability in rivalry dynamics across observers (Blake, Sobel, & Gilroy, 2003; Carter & Pettigrew, 2003). Second, notice that for each observer except H.E., the sphere was dominant, on average, for longer durations than was the grating. This outcome, too, dovetails with earlier work showing that motion promotes predominance during rivalry (e.g., Breese, 1909).

Of relevance for present purposes are the reliable differences between the manual and automatic conditions. For each observer, manual control of the motion of the sphere lengthened dominance durations of the sphere, relative to the durations on the automatic trials, and manual control abbreviated suppression durations of the sphere, again relative to the durations on the automatic trials. These differences in duration between the manual and automatic trials were highly significant statistically, as revealed by an analysis of variance (ANOVA) on logarithmically scaled data, $F(1, 364) = 12.95, p_{\text{rep}} > .99$, and $F(1, 364) = 12.79$, $p_{\text{rep}} > .99$, for the sphere-dominant and sphere-suppressed conditions, respectively. ANOVA also showed that the interaction between observer and condition was not statistically significant, $F(4, 364) = 2.17$, n.s., and $F(4, 364) = 0.95$, n.s., confirming that these differences were reliably present across observers. The effect size associated with manual control can be expressed as the percentage difference between the average

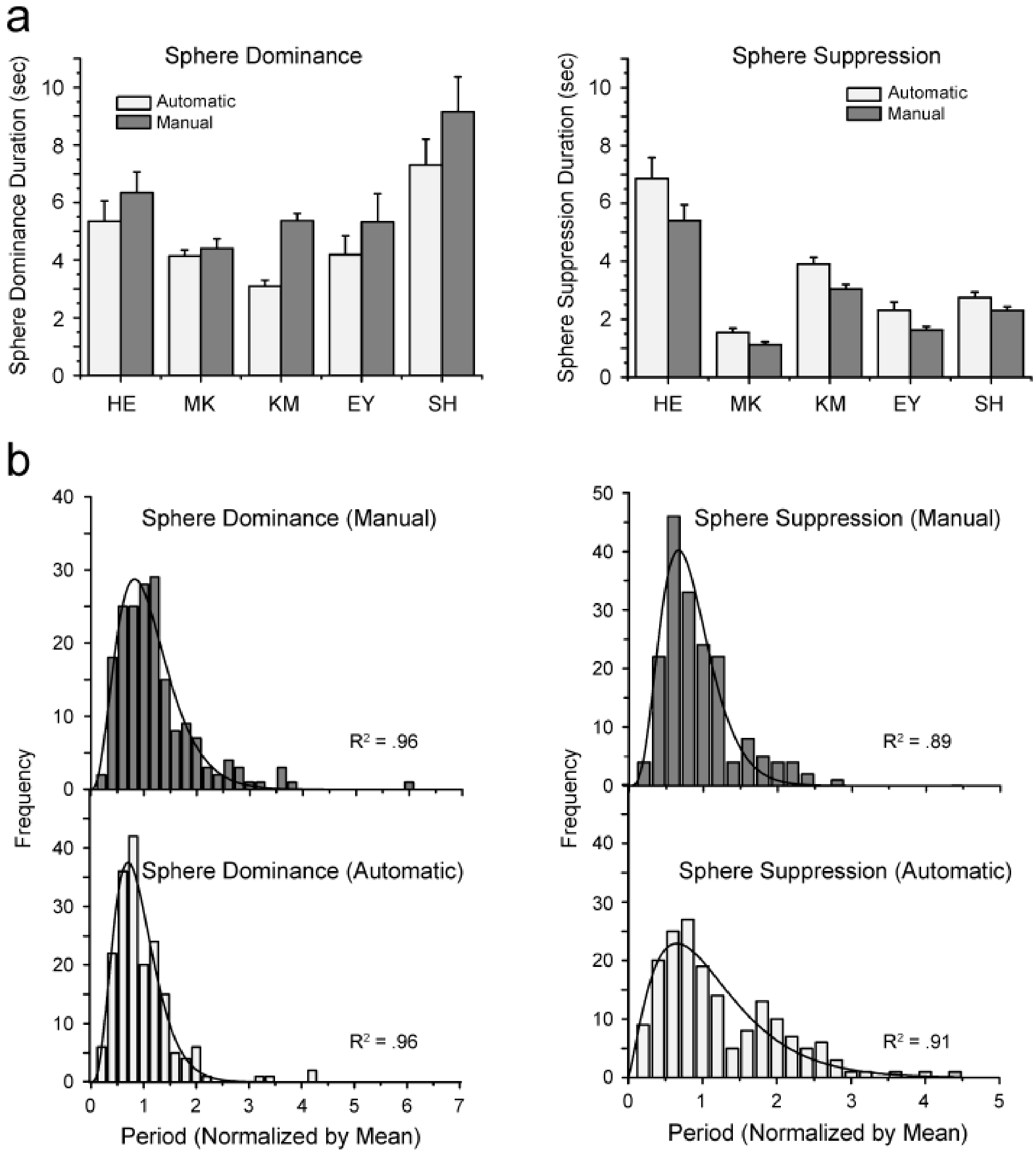

Fig. 3. Results from the main experiment. The graphs at the top (a) show the mean sphere-dominance (left) and sphere-suppression (right) durations in the automatic and manual conditions. Results are presented separately for each of the 5 observers. Error bars indicate standard errors of the means. The graphs in the lower two rows (b) show the distribution of normalized sphere-dominance (left) and sphere-suppression (right) durations, with results for the manual condition above results for the automatic condition. In each graph, the solid curve is the best-fit gamma distribution function, $f(x) = (\lambda^r / \Gamma(r))\, x^{r-1} \exp(-\lambda x)$; R^2 values are also given.

durations for the automatic and the manual conditions. Across observers, the effect size averaged 30% for the sphere-dominant condition and 27% for the sphere-suppressed condition.

This effect of stimulus control can also be seen in the frequency histograms shown in Figure 3b, which were compiled by normalizing each observer's individual dominance durations to the grand mean of all durations for that observer (thereby removing the between-observers variability in overall alternation rate). These histograms conform to the gamma distribution, a hallmark signature of binocular-rivalry data (Fox & Herrmann, 1967; Levelt, 1965; Logothetis, 1998), but the histograms for the two conditions—automatic versus manual—are displaced relative to one another, with the displacements in opposite directions for the sphere-dominant and the sphere-suppressed conditions. These results visually underscore the conclusions drawn from the average data and the ANOVA.

Discriminating Manual From Automatic Trials

It is natural to wonder whether observers were able to distinguish between manual and automatic trials and, if so, whether awareness of the difference between these two categories of trials might have contributed to the differences in the observed dominance durations. This is not a possibility, of course, for the sphere-suppressed condition, because the manual or automatic control was introduced when the grating, not the sphere, was visible; observers could not see the movements of the sphere until that rival target became dominant, at which time they immediately stopped moving the mouse. It is possible, however, that observers knew which condition was being tested on a given trial in the sphere-dominant condition, as they could see the sphere and judge its motion relative to the self-produced mouse movements. To assess observers' ability to discriminate manual control from automatic motion of the sphere, we calculated d' values from the observers' judgments of whether or not they had controlled the sphere's motion on each trial in the discrimination phase.

As one would expect, d' values tended to be higher for the 5-s than for the 3-s condition, because observers had more time to assess the correspondence between their own movements and those of the sphere. The d' values, averaged across the two exposure durations, varied from 2.0 to 3.7 across observers (see Table 1). There was, however, no direct relation between ability to discriminate the manual from the automatic condition and the magnitude of the influence of manual versus automatic control on dominance durations. Given this pattern of results, we are disinclined to believe that observers' dominance durations in the sphere-dominant condition were biased by knowledge about the particular trial type being tested on a given trial.

Replication With Automatic and Manual Trials in Random Order

We turn now to another potential source of bias. The data shown in Figures 3a and 3b were collected in blocks of eight trials, four manual trials followed by four automatic trials. Over trials, therefore, observers could have learned to predict which trial type was being administered on a given trial. This knowledge, in turn, could have encouraged observers to bias the durations of their mouse movements, and this bias could have produced the obtained pattern of results. There is no reason to think observers would purposefully try to do this (recall that 3 of the 5 observers were completely naive about the purpose of the experiment and, for that matter, were not explicitly aware of the existence of manual and automatic trials). Still, we felt it worthwhile to repeat the experiment, but with the manual and automatic trials randomly intermixed to preclude prediction of the upcoming trial type. We used the last movement record from the training phase, rather than movement data recorded from previous manual trials, to control the sphere's motion in the automatic trials. The same observers from the main experiment participated in this experiment, and they performed at least 50 trials in the dominance condition and at least 50 trials in the suppression condition.

Average dominance durations obtained in this modified replication are shown in Figure 4, and these results replicate those reported earlier: Dominance durations of the sphere were significantly longer on manual trials than on automatic trials in the sphere-dominant condition, $F(1, 571) = 71.73$, $p_{\mathrm{rep}} > .99$, and suppression durations of the sphere were significantly shorter on manual trials than on automatic trials in the sphere-suppressed condition, $F(1, 583) = 14.66$, $p_{\mathrm{rep}} > .99$. These results, obtained under conditions in which it was impossible to know which control condition was being tested, further substantiate the conclusion that the influence of manual control is not merely an effect of bias based on expectations or knowledge about the trial type.

TABLE 1

Observers' Ability to Discriminate Manual From Automatic Trials and the Magnitude of the Influence of Action on Dominance Durations

		Movement-duration ratio (manual/automatic)	
Subject	d' value	Sphere-dominant condition	Sphere-suppressed condition
M.K.	3.10 (2)	1.06 (5)	0.85 (5)
S.H.	2.62 (4)	1.25 (3)	0.79 (3)
H.E.	3.03 (3)	1.18 (4)	0.63 (2)
K.M.	2.00 (5)	1.73 (1)	0.81 (4)
E.Y.	3.72 (1)	1.27 (2)	0.60 (1)

Note. Ranks within group are given in parentheses. For the sphere-dominant condition, larger ratios denote a more robust effect of manual control; for the sphere-suppressed condition, smaller ratios denote a more robust effect of manual control.

DISCUSSION

Results from this study indicate that conflict between two incompatible visual stimuli tends to be resolved in favor of a stimulus that is under motor control of the observer viewing that stimulus. This outcome is consistent with the view that motor planning or execution (or both) influences visual perception, including in situations in which one is faced with conflicting interpretations about the nature of a visual object located in a given region of visual space (Leopold & Logothetis, 1999). Evidently conflict resolution takes into account the viewer's own motor intentions and the correspondence between those intentions and their actual outcomes. It is noteworthy that this influence of action on perception occurs even when the controlled stimulus is suppressed from awareness (i.e., when the other rival target is dominant exclusively). This aspect of our results rules out attention as the sole mediating factor, for the effect of control on the suppressed stimulus (which itself could not have been the focus of attention) was as large as the effect of control on the dominant stimulus.

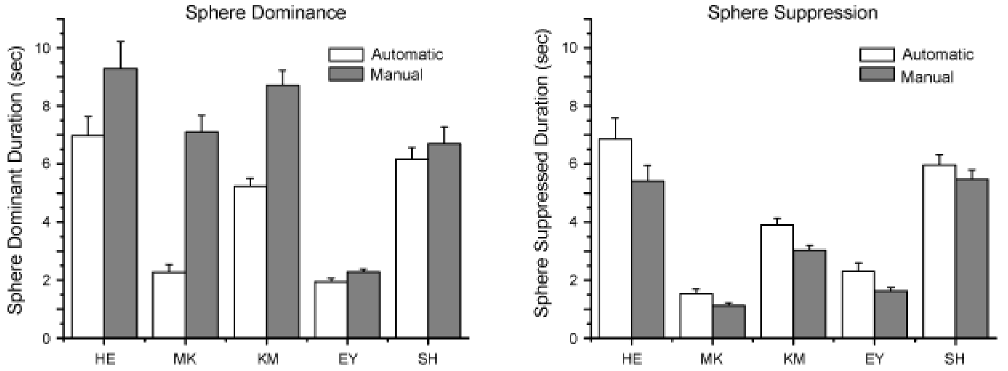

Fig. 4. Results from the control experiment. The graphs show the mean sphere-dominance (left) and sphere-suppression (right) durations in the automatic and manual conditions. Results are presented separately for each of the 5 observers. Error bars indicate standard errors of the means.

It is well established that the dynamics of binocular rivalry are governed by a host of stimulus variables—including contrast, motion, and figural complexity—that, together, fall within a category defined as "stimulus strength." In our study, motor control behaved as if it, too, belonged in this category. But by what means could motor control affect the stimulus strength of a rival target? One reasonable hypothesis can be derived from the widely held view that visually guided actions are mediated by neural events in brain areas forming the so-called dorsal-stream pathway (Goodale & Milner, 1992). Among other things, this pathway is specialized for visuo-motor transformations underlying motor planning of intentional actions (Andersen & Buneo, 2002). It is also known (Fang & He, 2005) that neural activity within this pathway remains strong during both dominance and suppression phases of binocular rivalry, unlike activity in the ventral-stream pathway, where activity fluctuates during rivalry. Thus, it is conceivable that during both dominance and suppression phases, actions and their visual consequences are registered within dorsal-stream structures involved in the control of visually guided actions. Through feedback, lateral interconnections, or both, this dorsal-stream activity, in turn, could modulate neural events in brain areas where rivalry does transpire.

Whatever the underlying neural circuitry supporting the boost that motor control conveys to the effective strength of a rival target, our findings add to the emerging view of binocular rivalry as a complex phenomenon mediated by hierarchically organized neural sites (Blake, 2002; Blake & Logothetis, 2002; Dayan, 1998), including brain areas involved in planning and execution of motor actions. Remarkably, our results also imply that one need not be consciously aware of the visual consequences of those actions for this influence to be exerted: We observed that a dynamic visual event's transition from suppression to dominance tended to occur more quickly when the dynamics of the event were self-initiated, even though observers could not visualize the consequences of their own actions. Thus, our findings are consistent with the view that aspects of self-initiated control can be monitored outside of awareness (Botvinick et al., 2001).

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