Voluntary control and the dynamics of perceptual bi-stability

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Abstract

Voluntary control and conscious perception seem to be related: when we are confronted with ambiguous images we are in some cases and to some extent able to voluntarily select a percept. However, to date voluntary control has not been used in neurophysiological studies on the correlates of conscious perception, presumably because the dynamic of perceptual reversals was not suitable. We exposed the visual system to four ambiguous stimuli that instigate bi-stable perception: slant rivalry, orthogonal grating rivalry, house-face rivalry, and Necker cube rivalry. In the preceding companion paper [van Ee, R. (2005). Dynamics of perceptual bi-stability for stereoscopic slant rivalry and a comparison with grating, house-face, and Necker cube rivalry. *Vision Research*] we focussed on the temporal dynamics of the perceptual reversals. Here we examined the role of voluntary control in the dynamics of perceptual reversals. We asked subjects to attempt to hold percepts and to speed-up the perceptual reversals. The investigations across the four stimuli revealed qualitative similarities concerning the influence of voluntary control on the temporal dynamics of perceptual reversals. We also found differences. In comparison to the other rivalry stimuli, slant rivalry exhibits: (1) relatively long percept durations; (2) a relatively clear role of voluntary control in modifying the percept durations. We advocate that these aspects, alongside with its metrical (quantitative) aspects, potentially make slant rivalry an interesting tool in studying the neural underpinnings of visual awareness.

1. Introduction

In some cases, we are able to influence our visual perception when confronted with ambiguous images. Although it takes effort, and although our control is limited, we are able to influence the perceptual reversals when we are confronted with certain ambiguous images that generate bi-stable perception. The extent to which voluntary control influences the frequency of perceptual reversals seems to be a useful quantifiable feature. However, to date none of the existing neurophysiological studies on the correlates of bi-stable perception utilized the phenomenon of voluntary control. [1]

Although explicit subjective accounts of voluntary control occurred over hundred years ago (Breese, 1899; Helmholtz von, 1866; McDougall, 1903; Wheatstone, 1838) [2] the literature on systematic voluntary

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[1] This control concerns one out of two competing percepts (either of them depending on constituting signals) and does not concern the penetration of a percept to alter how signals are being integrated (for discussion see Pylyshyn, 1999).

[2] Wundt presented seminal work on the role of eye movements and rejected voluntary control as the cause for perceptual reversals in ambiguous stimuli (Wundt, 1898). We now know that, although eye movements may help, the preponderance of evidence indicates that (micro)saccades, blinks and vergence are not essential for a perceptual reversal. We come back to this issue in the discussion section.

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control experiments is surprisingly sparse. None of the extant voluntary control studies made use of a metrical (quantitative) paradigm in which the parameters that govern the perceptual reversal changed in a parametric way (pixel-by-pixel, say). In an attempt to study how a voluntarily selected percept—in our case a perceived slant—is related to the metrical aspects of the constituting signals we have recently developed a slant rivalry paradigm. The slant rivalry paradigm capitalizes on depth cue integration of disparity and perspective in stereoscopic vision (van Ee, Adams, & Mamassian, 2003; van Ee, van Dam, & Erkelens, 2002). [3] In the preceding companion paper (van Ee, 2005) we have compared the dynamics of slant-rivalry with a number of classical rivalry paradigms. Here we will use the same paradigms for a comparison of the role of voluntary control. The paradigms that we studied for comparison with our slant rivalry paradigm include binocular rivalry, namely orthogonal grating rivalry (Breese, 1899) and house-face rivalry (Tong, Nakayama, Vaughan, & Kanwisher, 1998), as well as Necker cube rivalry (Necker, 1832).

There are numerous indications in the literature suggesting that the perceptual reversal frequency is under some kind of influence that may be cognitive. For example, for stimuli that contain reversible perspective it has been reported that the perceptual reversal rate depends on the familiarity of the stimulus (Donahue & Griffitts, 1931; Washburn, Reagan, & Thurston, 1934), the influence of drugs (Phillipson & Harris, 1984), adaptation (Harris, 1980; Long & Toppino, 1994; Virsu, 1975), spatial attention (Flügel, 1913), instruction (Liebert & Burk, 1985), and concentration (Reisberg & O'Shaughnessy, 1984). Similarly, for binocular rivalry the reversal rate depends on the effect of instructions (Lack, 1978; Meredith & Meredith, 1962), familiarity of the object (Yu & Blake, 1992), the use of drugs (Barany & Hallden, 1947), learning (Lack, 1969) and attention (Helmholtz von, 1866; Ooi & He, 1999). For the Necker cube it has been reported that the reversal rate depends on attention (Kawabata, 1986), the configuration of multiple cubes (Adams & Haire, 1958), psychiatric abnormal-

ities (Hunt & Guilford, 1933), brain lesions (Bisiach, Ricci, Lai, De Tanti, & Inzaghi, 1999; Cohen, 1959b) and effort of will (Taddei-Ferretti, Musio, Santillo, & Cotugno, 1999). In addition, for other types of ambiguous figures similar findings have been reported on attention (Hol, Koene, & van Ee, 2003; Tsal & Kolbet, 1985), familiarity of the object (Strüber & Stadler, 1999), culture (Bagby, 1957), imagining (Horlitz & O'Leary, 1993), knowledge (Rock & Mitchener, 1992), and brain lesions (Ricci & Blundo, 1990). For a number of ambiguous stimuli perceptual trapping has been reported (Ooi & He, 2003; Suzuki & Grabowecky, 2002); perceptual trapping brings about a recurring pattern of reversals thereby overriding spontaneous reversals.

Although there is a wealth of data on the role of cognitive influence on perceptual reversals in bi-stability, systematic voluntary control studies are sparse. Further, the published studies have suffered from a lack of agreement in methods and data analysis. In the present study we analyse a wide spectrum of data that have been collected under experimental conditions that are as identical as reasonably possible.

The results on the voluntary control comparisons across the used stimuli were first presented at conferences of which the abstracts appeared in the Journal of Vision (van Ee, 2002; van Ee, van Dam, Brouwer, & Korsten, 2003).

2. Methods

A considerable part of the methods is identical to those described in the preceding accompanying paper. The identical part will be described briefly.

2.1. Experiment 1

2.1.1. Stimuli and apparatus

Experiment 1 concerns the dynamics of voluntary control for slant rivalry. The icons in the figures of this paper illustrate the stimulus (Fig. 1a of the preceding accompanying paper illustrates the stimuli in greater detail, and at www.phys.uu.nl/~vanee/ several anaglyphic versions of the slant rivalry stimulus can be viewed). The stimulus was presented dichoptically using red-green glasses enabling us to produce disparity-specified slant independently of the perspective-specified slant. The width of the trapezoid was 1.2°. The correct perspective and disparity distortions of the stimuli were generated using OpenGl libraries. The combinations of perspective- and disparity-specified slants were ($-70°$, 56° and 70°, $-56°$). Subjects were seated at a viewing distance of 114 cm. The aperture in which the trapezoid was presented measured $1.8° \times 1.8°$. Subjects were requested to keep their fixation within a central rectangle ($0.6° \times 0.4°$) of a sunburst-like fixation symbol.

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[3] By adding disparity to the Necker cube (Cormack & Arger, 1968) and rotating cylinders or globes (Nawrot & Blake, 1991; Parker, Krug, & Cumming, 2003) one can selectively alter the appearance: In those stimuli disparity can in principle be brought in conflict with monocular depth cues in a metrical fashion. In fact, the Necker cube (but in some sense also the rotating object) is a special case of our slant rivalry stimulus, having additional constraints through which disparity and perspective are related by Gestalt or figural cues. Note that the Necker cube is not a correct representation of a real 3D cube and yet we perceive it as a cube. In pilot studies we found that disparity did not have a parametrically well-predictable effect on bi-stable perception of the Necker cube, which is supported by findings from the literature (e.g. Cormack & Arger, 1968), probably because observers have a preference to perceive symmetrical figures like square cubes.
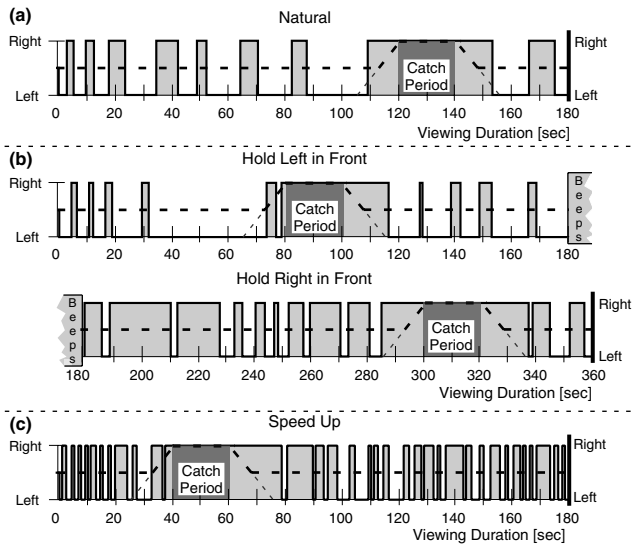
Fig. 1. Voluntary control and the time series of perceptual reversals. Examples of raw data. Subject LW viewed the slant rivalry stimulus while he exerted different control tasks. For the data in (a) LW viewed the stimulus for 3 min in a natural way without attempting to control the reversal rate. For the data in (b) LW viewed the same stimulus for 6 min while he attempted to first hold the left side in front for 3 min and then to hold the right side in front for another 3 min. The onset of the second 3-min period was indicated by beeps. The data demonstrate that LW is clearly able to exert control over the stimuli, but spontaneous reversals could not be prevented. The data in (c) were collected while LW attempted to speed-up the perceptual reversal rate, leading to an increased frequency of perceptual reversals.

2.1.2. Task

The stimulus onset was initiated by a mouse click. While keeping their gaze within the sunburst symbol the subjects reported their perceptual reversals using two keyboard keys. One key signalled that the left side was perceived in front, the other key that the right side was perceived in front. To investigate systematically whether subjects are able to voluntarily control the rate of the alternative percepts, we asked the subjects to engage in different control-exertion tasks:

(1) Natural: In one presentation block subjects were asked to view the stimulus for 3 min in a natural (or sometimes called "habitual") way, without attempting to control the reversal rate.
(2) Hold: In another presentation block subjects were asked to view the same stimulus for 6 min and, first, to attempt to hold the left side in front for 3 min, and then, second to attempt to hold the right side in front for another 3 min. The transition from the first to the second 3 min was clearly signalled by three beeps.
(3) Speed-up: In a third presentation block subjects were asked to view the stimulus for 3 min and to attempt to maximize the perceptual reversal rate.

The hold exertion task has been explored previously (Breese, 1899; Gómez, Argañdona, Solier, Angulo, & Vázquez, 1995; Hochberg & Peterson, 1987; Lack, 1969, 1978; McDougall, 1903; Meredith & Meredith, 1962; Pelton & Solley, 1968; Peterson & Hochberg, 1983; Peterson, 1986; Strüber & Stadler, 1999; Suzuki & Peterson, 2000; Toppino, 2003; Washburn et al., 1934). It should be noted though that quite some studies failed to do the appropriate controls for a complete interpretation in terms of both the number of reversals and the period that one of the percepts dominated (see also Lack, 1978): Subjects could follow the hold instructions either by increasing the dominance durations for one pattern (decreased number of fluctuations) or decreasing the durations for the other pattern (increased number of fluctuations).

Few studies have experimentally compared, but only for one stimulus, the natural, hold, and speed-up control exertions tasks (Bruner, Postman, & Mosteller, 1950; Glen, 1940; Phillipson & Harris, 1984). More relevant is that some studies have explicitly compared the role of voluntary control of the reversal rate for the Necker cube and for binocular rivalry (George, 1936; Meredith, 1967; Vernon, 1937; Washburn & Gillette, 1933; see also for discussion McDougall, 1906; Meredith & Meredith, 1962).

2.1.3. Procedure

We randomised for the sign of the surface slant as well as for both anaglyph colour, and for left and right eye presentation. For each of the three control-exertion tasks there were four presentation blocks (permutations of positive and negative surface slant sign as well as permutations of red and green filters in front of the left eye). The randomisation gave, thus, rise to 12 different presentation blocks. Using a visual slant estimation method (van Ee & Erkelens, 1996) we asked subjects to estimate the slant that was perceived during the stimulus presentation so that we knew that the subject was able to experience bi-stability in the appearance of the grid. We did so after each presentation block.

The rivalrous stimuli were intermixed with periods of non-rivalrous stimuli (see Fig. 2a of accompanying paper). In a catch period the disparity specified slant was identical to the perspective-specified slant and no perceptual reversals were expected to occur during that period of non-rivalrous stimulation. The data collected during the catch period were used to check whether the subjects were reporting their perceptual states reliably, rather than pressing keys at random. In practice, we found that on average only 1 out of 83 data blocks had to be discarded because the performance in the non-rivalrous period was below 90%. This emphasizes that subjects were reliably consistent in their pattern of responses. To ensure that the subject was unable to anticipate the onset of the catch period we applied three
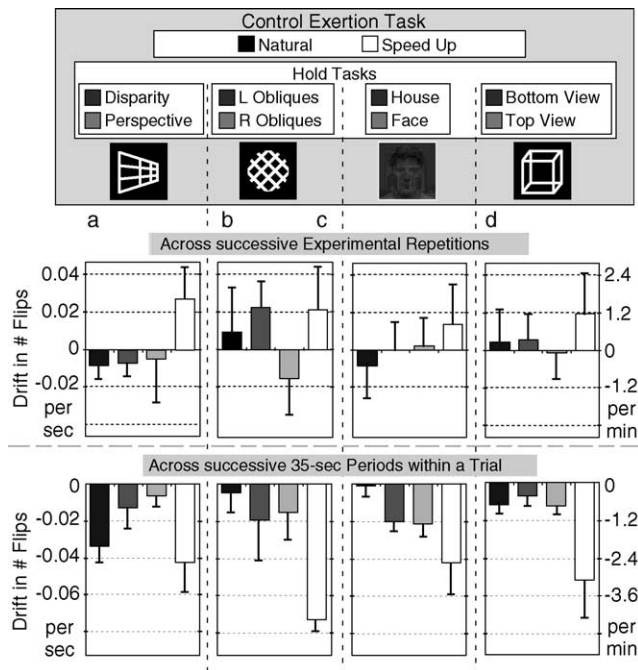
Fig. 2. Flip rate drift across different control exertion tasks for the four rivalry stimuli. The top panels show the mean reversal (called flip) rate drift across successive experimental repetitions for the six subjects for (a) the slant rivalry stimulus, (b) the orthogonal grating, (c) the house-face, and (d) the Necker cube stimulus. The icons specify the stimuli for which the data is being presented. For the speed-up control exertion task there is a consistent increase in the flip rate. The bottom panels illustrate that there is a decrease in the number of flips per second across 35-s portions: the flip rate is larger after the start of a trial than during the course of the series. For the four rivalry stimuli the data patterns seem to be quite similar. Error bars represent standard errors across the six subjects. In this figure, and in the next figures in which we compare the different stimuli, we use dark grey to indicate one hold control exertion task and light grey to indicate the alternative hold task. Black and white bars indicate the natural and the speed-up control exertion task, respectively.

different onsets of the catch period for each control-exertion task. This, in turn, means that for each control-exertion task the subject ran three presentation blocks.

This catch procedure (producing 3 different blocks) in combination with the above-described randomisation procedure (producing 12 different blocks) gave rise to 36 different presentation blocks. These 36 blocks were subdivided into six experimental sessions. In three of the sessions the subjects wore the red filter over the left eye and the green filter over the right eye. In the other three sessions the filters were reversed. Each of the six experimental sessions ran for 24 min—subtended by, in order, 2 times 3 min for the *Natural* control-exertion blocks, 2 times 6 min for the *Hold* control-exertion task blocks, and 2 times 3 min for the *Speed-up* control-exertion task blocks. For the first of each pair of blocks that were devoted to a particular control-exertion task the

perspective-specified slant was always positive, and in the second block it was always negative.

Two complete repetitions of the experiment (12 sessions of 24 min) were performed by each subject. Two subjects (LW and NK) did twice as many sessions to get a better indication of the variability in performance.

2.1.4. Subjects and data analysis

The same subjects from the accompanying paper participated. The collected raw data indicated whether either the left side or the right side of the wire frame grid was perceived in front. We further analysed the data in terms of disparity-slant-dominated and perspective-slant-dominated perceptual durations by using a record that related the side that was perceived in front to the disparity-specified or the perspective-specified slant. For each control-exertion task we examined the drift of the reversal process across successive experimental repetitions and across successive 35-s portions of data. For completeness, an analysis of drift should be part of the analysis of time series of variable processes. After we established that the drift was not unreasonably large we determined the percentage of time that one of the two alternative percepts was present.

We also determined the relative number of reversals. To interpret the data on percept dominance it is essential to also study the number of reversals. It may be possible for subjects to follow the hold instructions either by increasing the separate durations of the held pattern (resulting in a decreased number of fluctuations) or decreasing the durations for which the other pattern is seen (resulting in an increased number of fluctuations). For discussions on this issue see Lack (1978).

Finally we determined the percept duration for each subject across the different control-exertion tasks.

2.2. Experiment 2

To compare the role of voluntary control for the trapezoid stimulus with classical rivalry stimuli we repeated Experiment 1 with different stimuli. The rivalrous stimuli of Experiment 2 consisted of orthogonal gratings, house-face stimuli, and the Necker cube (see the icons in the figures or for more detail Fig. 1b–d of the accompanying paper). The stimuli subtended 1.2°, which is the same size as used in Experiment 1. The orthogonal gratings stimuli consisted of four oblique lines that had perpendicular orientations (45° with the vertical) in the two eyes. The spatial frequency of the gratings was 3.3 cycles per degree. The house-face stimuli were identical to those developed by Tong (Tong et al., 1998). The Necker cube stimulus was presented anaglyphically (but with zero disparity), so that the stimulus presentation of the other stimuli was resembled.

The instructions to the subjects were also identical to those of Experiment 1. For the orthogonal grating stim-

ulus the subjects were instructed to press one key when they perceived the left obliques (lines under 45° going from top left to bottom right) and to press another key when they perceived the right obliques (going from top right to bottom left). Subjects were instructed to concentrate on the central area of the patch. For the house-face stimulus subjects were instructed to press one key when the house was perceived in the central region of the stimulus, and to press another key when the face was perceived. For the Necker cube subjects pressed one key when they perceived the cube as if they viewed it from below and another key when they perceived the cube as if they viewed it from above.

Subjects first participated in a complete experiment for the trapezoid stimulus (six sessions in Experiment 1) before they started the orthogonal grating experiment. Again they completed six sessions before they started the house-face experiment and again they completed six house-face sessions before they started the Necker cube experiment. Then a repetition of the four stimuli began. In other words, for each stimulus two complete experiments (12 sessions of 24 min) were conducted (in all 48 sessions). Two subjects did twice as many sessions to get a better indication of the variability in performance across experiments. In all, the six subjects ran a total of 384, 24-min sessions.

The six subjects from Experiment 1 participated. To compare the subjects' performance across the four stimuli we compared the means of (1) perceptual reversal rate drift across experimental repetitions, (2) reversal rate drift within data blocks, (3) the percentages of time that one of the alternative percepts was present, as well as (4) the percept durations and the number of reversals.

3. Results

We first examined the influence of voluntary control on the stability of the perceptual reversals over time. Then we consider its influence on the percent of time that a percept is present and finally we look at the percept durations. Note that the data for the natural control exertion task (the black bars of Figs. 2–4) have been presented previously in the accompanying paper. The presented results are based upon a total of 59.589 perceptual reversals.

3.1. Results and discussion of Experiment 1

Fig. 1 compares examples of raw data of subject LW. Panel a depicts the data for the natural control exertion task. In panel b we see that LW was able to follow the control exertion instruction "try to hold the left side in front". But spontaneous perceptual reversals could not be prevented. After 180 s into this data collection block, beeps were produced and the control exertion instruc-
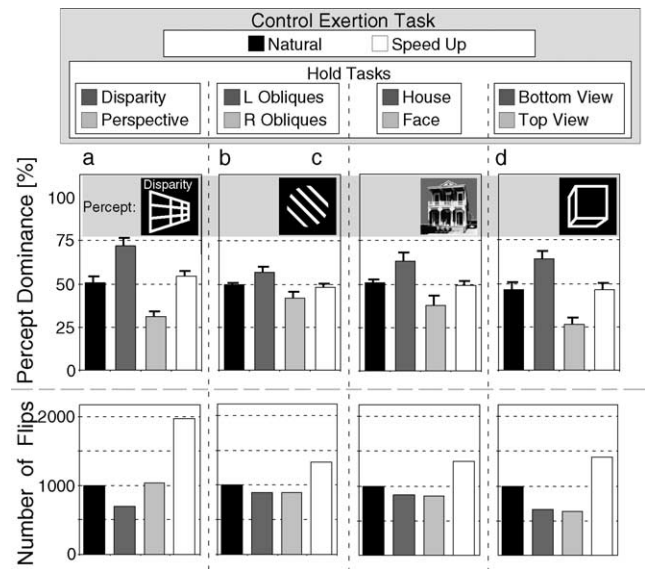

Fig. 3. Voluntary control on percept presence for the four rivalry stimuli. The top panels show the mean percept dominance across the six subjects for (a) the slant rivalry stimulus, (b) the orthogonal grating, (c) the house-face, and (d) the Necker cube stimulus. The percepts for which we plotted the dominance percentages are specified by the icons. Error bars represent standard errors. The bottom panels portray the relative number of flips for our stimuli. In terms of the number of flips, subjects seem to have slightly more control over the slant-rivalry stimulus than over the other stimuli.

tion then became "try to hold the right side in front". Again we see that LW is clearly able to follow this instruction. In the speed-up task (panel c) there were relatively many perceptual reversals. During the catch periods in which the disparity and the perspective specified slant were congruent, he did not experience perceptual reversals. LWs complete data for Experiment 1 consisted of 48 times as much data as depicted in Fig. 1. From the raw data (such as in Fig. 1) we determined the perceptual durations for the left front and the right-front percepts. After taking into account the sign of the surface slant, the data indicated whether either the perspective-specified or the disparity-specified slant dominated.

Fig. 2a presents the mean drift in the data, across the six subjects for Experiment 1. These average data are based upon a total of 16.522 perceptual reversals. The top panel portrays the mean reversal rate drift across successive experimental repetitions. For the Natural and the hold tasks there is a slight decrease in the number of reversals per second. For the speed-up task there is an increase in the reversal rate of about 1 reversal per minute. The bottom panel illustrates that there is a decrease in the number of reversals per second across 35-s portions. Whenever a data collection series starts, the reversal rate is larger than during the course of the series. Although the drift is on the order of 0.02 reversals per second across experimental repetitions for the
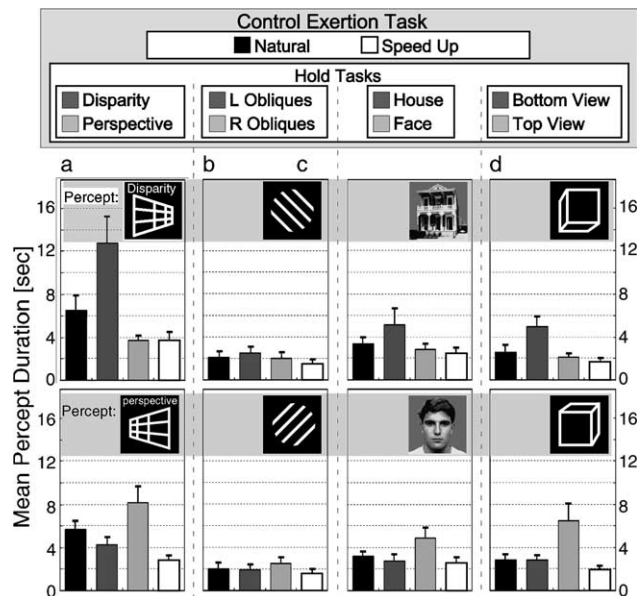
Fig. 4. Voluntary control on percept duration for the four rivalry stimuli. The mean percept durations across the six subjects for (a) the slant rivalry stimulus, (b) the orthogonal grating, (c) the house-face, and (d) the Necker cube stimulus. The stimuli for which we plotted the durations are specified by the icons. The influence of voluntary control on the different control-exertion tasks for both the grating stimulus and the house-face stimulus was not significant. For the Necker cube we find an influence of voluntary control that is significant, and speaking in relative terms, comparable to the slant rivalry. However, in absolute terms the percept durations in the Necker cube stimulus are about 2.5 times shorter than for the slant stimulus. Error bars represent standard errors.

speed-up control task, the majority of the reversal rate data are reasonably stable for a process that is variable in nature.

The top panel of Fig. 3a presents the mean percentages of time that the disparity-dominated percept was present for the different control-exertion tasks. These data show that subjects were very well able to voluntarily hold both the disparity-dominated percept and the perspective-dominated percept (72.2% vs. 50.7%, $F(1,10) = 30.6$, $p = 0.0002$ and 31.1% vs. 50.7%, $F(1,10) = 0.001$, respectively). We did not find a significant difference in perceptual-dominance between the natural condition and the condition in which subjects attempted to speed-up the perceptual reversals. This implies that attempting to speed-up perceptual reversals does not influence the dominance of one percept over the other.

From the data in the top panel of Fig. 3 it is not clear whether the subject is voluntarily able to alter the number of reversals. The lower panel of Fig. 3a presents the number of perceptual reversals for the control-exertion tasks. The number of reversals for the natural task is normalized to 1000. The data show that the subjects are able to hold the disparity-specified percept by bringing down the number of reversals to the alternative

percept. Interestingly, to hold the perspective-dominated percept, the subjects do not bring down the number of reversals from the perspective to the disparity-dominated percept (note that the number of reversals for the hold-perspective slant is about equal to the number of reversals for the natural control-exertion task.) Instead, reducing the periods that the disparity-dominated percept was present has produced the increase in the percentage of the perspective-dominated percept. The subjects are clearly able to increase the number of reversals in the speed-up task. Note that, even though there are about twice as many perceptual reversals, the average percentage of time that the disparity-dominated percept is present for the speed-up task is only slightly larger than for the natural task. In Table 1 the disparity percept dominances are presented for the individual subjects. [4]

Fig. 4a presents the average means for the different control-exertion tasks for both the disparity-dominated (top panel) and the perspective-dominated (bottom panel) percept durations. For the natural control-exertion task the mean of the distribution for the disparity-percept durations is 6.3 s. The second bar shows that the subjects are voluntarily able to increase the mean up to 12.9 s when they attempt to hold the disparity-dominated percept ($F(1,10) = 6.4$, $p = 0.03$). The third bar shows that the subjects are able to decrease the mean down to 3.6 s when they attempt to hold the perspective-dominated percept ($F(1,10) = 6.6$, $p = 0.03$). Attempting to speed-up the perceptual reversals significantly decreases the percept duration relative to the natural control exertion task. (3.6 s vs. 6.3 s, $F(1,10) = 7.3$, $p = 0.02$). The disparity-dominated percept duration for the hold perspective and the speed-up control exertion tasks are identical, indicating that subjects used a similar way to abandon the unwanted percept. For the perspective-dominated percept durations (bottom panels) the mean of the distribution for the natural control-exertion task is 5.6 s. The second bar shows that the subjects are able to decrease the mean to 4.1 s when they attempt to hold the disparity-dominated percept ($F(1,10) = 5.7$, $p = 0.04$). Attempting to hold the perspective-dominated percept increases the percept duration (8.2 s vs. 5.6 s). Finally, attempting to speed-up the perceptual reversals significantly decreases the mean for the perspective-dominated percept (2.8 s vs. 5.6 s, $F(1,10) = 17.1$, $p = 0.002$). In Table 2 the percept durations are presented for the individual subjects. There is considerable variation across subjects, just as has been reported previously for other paradigms (Aafjes, Hueting, & Visser, 1966; Bruner et al., 1950; Frederiksen &

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[4] Elsewhere we (Koene & van Ee, in press) presented a neural network model that produces the data patterns found. However, obviously other models are possible and the data of Table 1 (as well as those in Table 2) can be used for future modeling purposes.

Table 1
Percept dominance: the percept dominances across the individual subjects for the different rivalry stimuli

Percept dominance [%]

Rivalry	Control exertion	LW	NK	MS	LD	GB	SV	Mean	Standard error
Slant (disparity-dominance)	Natural	51.0	53.4	62.9	46.0	45.4	45.6	50.7	3.0
	Hold disparity	79.0	77.7	83.5	63.2	61.7	67.9	72.2	4.1
	Hold perspective	24.2	36.6	30.0	38.5	30.3	27.2	31.1	2.4
	Speed-up	55.0	51.9	62.0	60.1	46.3	49.8	54.2	2.7
Grating (left obliques dominance)	Natural	49.8	48.3	51.6	49.6	50.2	48.2	49.6	0.6
	Hold L obliques	64.6	59.5	52.6	53.7	48.6	62.6	56.9	2.8
	Hold R obliques	37.9	39.2	39.0	50.3	50.4	35.3	42.0	3.0
	Speed-up	48.1	49.3	42.4	50.9	49.9	48.8	48.2	1.3
House-face (house dominance)	Natural	54.4	51.1	47.5	54.5	51.4	46.9	51.0	1.5
	Hold house	79.7	61.8	56.9	61.4	50.8	68.9	63.3	4.5
	Hold face	25.4	35.7	33.2	52.1	50.4	30.4	37.9	4.9
	Speed-up	42.1	54.3	46.2	51.1	53.2	48.8	49.3	2.1
Necker cube (bottom dominance)	Natural	55.7	50.6	32.4	42.6	45.2	52.1	46.4	3.7
	Hold bottom	72.0	63.3	57.4	52.5	64.6	75.0	64.1	3.8
	Hold top	27.6	17.5	15.5	35.7	33.0	28.3	26.3	3.6
	Speed-up	55.5	47.4	36.3	37.7	48.9	52.3	46.4	3.5

Guilford, 1934; Sadler & Mefferd, 1970). For example, for SV the percept duration for the hold disparity task is 17.0 s. For GB and LD this percept duration is only 8.2 s and 4.2 s, respectively.

An analysis of the estimated slant for each individual data block revealed that the subjects were able to perceive bi-stability for all slant stimuli presented. The reported slants resembled those reported previously (van Ee, 2005).

3.2. Results and discussion of Experiment 2

To compare the dynamics of voluntary control for the slant rivalry stimulus with a number of conventional ambiguous stimuli, we performed the above-described analyses for the orthogonal grating stimulus, the house-face stimulus, and the Necker-cube. The results of Experiment 2 are based upon a total of 43.067 perceptual reversals (without slant rivalry reversals).

Fig. 2b–d show the mean reversal (called flip) rate drift during the experiment for the orthogonal grating rivalry, the house-face rivalry, and the Necker cube rivalry, respectively. The top panels of Fig. 2b–d illustrate the drift in flip rate across successive experimental repetitions. The increase in flip rate for both the house-face stimulus and the Necker cube are not significantly different from zero. There are only a few accounts in the literature for comparison: Lack found for the orthogonal grating an increase of 0.06 flips per second for the speed-up task (Lack, 1969), which is comparable to what we found. Ulrich and Ammons examined practice effects for the flip rate for the Necker cube. It is hard to make a quantitative comparison with their data. Qualitatively, they too, reported an increase in the rate over days

(Ulrich & Ammons, 1960). The bottom panels of Fig. 2b–d illustrate the increase in flip rate across successive 35-s portions. Whenever a data collection series starts the flip rate is larger than during the course of the series. For the speed-up control exertion task for the grating the decrease is 0.07 flips per second. The only account in the literature that studied the same stimulus as we did, reported an identical decrease of 0.07 flips per second (Lehky, 1995). For a horizontal-vertical line binocular rivalry stimulus a negative change in the flip rate under natural viewing has been reported (Cogan & Goldstein, 1967; Wade, 1975), just as we found. For the Necker cube, however, most accounts in the literature that addressed the flip rates across short periods of data, report a (relatively small) rate increase (Babich & Standing, 1981; Cohen, 1959a; Toppino & Long, 1987). These values were supposedly for the natural control exertion task. Further, it has been reported that for the hold task the change is not significantly different from zero and for the speed-up task the change is positive (Pelton & Solley, 1968). For the speed-up task a considerable increase in the flip rate has been reported (Ammons, Ulrich, & Ammons, 1960). The drift for the speed-up condition is consistently larger than for the natural condition, meaning that the drift is not dependent on the observation period but rather on the rate or the total number of flips. Future models should be consistent with this finding. In general, the data pattern we found for the four rivalry stimuli seem to be quite similar. Note that the drift across sessions is smaller ($p < 0.08$) than within a session. During each trial the reversal rate starts relatively fast and then slows down. On another trial, which might be on another day, this slow down pattern repeats itself.

Table 2
Percept durations: the percept durations across the individual subjects for the different rivalry stimuli

Percept durations [s]

Rivalry	Control exertion	One percent dominance								Alternative percept dominance							
		LW	NK	MS	LD	GB	SV	Mean	Standard error	LW	NK	MS	LD	GB	SV	Mean	Standard error
		Disparity								*Perspective*							
Slant	Natural	6.9	5.6	11.9	2.9	4.5	6.3	6.3	1.4	6.0	4.7	7.1	3.5	4.8	7.5	5.6	0.7
	Hold disparity	16.2	15.6	16.2	4.2	8.2	17.0	12.9	2.4	4.0	3.2	4.2	2.4	4.4	6.6	4.1	0.6
	Hold perspective	3.8	2.9	4.6	2.4	3.8	4.1	3.6	0.4	9.9	5.6	12.0	3.9	7.4	10.2	8.2	1.4
	Speed-up	2.9	2.5	7.1	2.7	3.7	2.9	3.6	0.8	2.4	2.3	3.6	1.8	3.7	2.8	2.8	0.3
		Left obliques								*Right obliques*							
Grating	Natural	1.6	1.8	3.5	1.1	3.3	1.1	2.1	0.5	1.5	1.8	3.4	1.2	3.1	1.2	2.0	0.4
	Hold L obliques	2.7	2.0	3.9	1.1	3.3	2.1	2.5	0.4	1.5	1.4	3.3	1.0	3.0	1.2	1.9	0.4
	Hold R obliques	1.6	1.3	3.3	1.1	3.4	1.3	2.0	0.5	2.5	2.0	4.1	1.1	3.0	2.3	2.5	0.5
	Speed-up	1.2	1.2	1.9	0.9	2.8	0.9	1.5	0.3	1.2	1.2	2.6	0.9	2.7	0.9	1.6	0.4
		House								*Face*							
House-face	Natural	5.2	3.6	3.2	2.9	3.9	1.7	3.4	0.5	4.1	3.4	3.5	2.4	3.6	1.9	3.2	0.4
	Hold house	11.2	3.5	5.2	3.0	4.6	3.6	5.2	1.4	2.6	2.2	3.7	1.9	4.4	1.7	2.7	0.5
	Hold face	3.0	2.1	3.1	2.5	4.5	1.9	2.8	0.4	8.3	3.8	6.0	2.3	4.4	4.3	4.8	0.9
	Speed-up	2.6	2.0	2.4	2.2	4.2	1.4	2.5	0.4	3.6	1.7	2.8	2.1	3.8	1.5	2.6	0.4
		Bottom view								*Top view*							
Necker cube	Natural	4.9	3.4	1.9	1.6	2.2	1.4	2.6	0.6	4.1	3.3	3.5	2.1	2.6	1.3	2.8	0.5
	Hold bottom	7.7	5.9	4.7	2.1	4.4	5.2	5.0	0.8	3.0	3.9	3.6	1.9	2.7	1.8	2.8	0.4
	Hold top	3.2	2.3	1.8	1.5	2.2	1.6	2.1	0.3	8.1	11.5	7.9	2.7	4.4	3.9	6.4	1.5
	Speed-up	2.7	1.6	1.6	1.2	1.9	1.0	1.7	0.3	2.2	1.8	2.7	2.0	2.0	0.9	1.9	0.3

Fig. 3b–d compare the average percentages of percept dominance (top panels) as well as the relative number of flips (bottom panels) for the orthogonal grating rivalry, the house-face rivalry, and the Necker cube rivalry, respectively. Fig. 3b shows that holding the left obliques significantly increases the perceptual dominance for this percept (56.9% vs. 49.6%, $F(1, 10) = 7.6$, $p = 0.02$). Holding the right obliques had the opposite effect (42.0% vs. 49.6%, $F(1, 10) = 7.9$, $p = 0.02$). Similarly to what we found for the trapezoid stimulus, we found no significant difference in perceptual dominance between the natural condition and the condition in which subjects attempted to speed-up the perceptual reversals. The lower panel of Fig. 3b presents the relative number of perceptual reversals across the control-exertion tasks. The subjects seem to hold either of the two percepts by bringing down the number of flips to the alternative percept. The number of flips increased for the speed-up task. Fig. 3c shows that holding the house percept significantly increases the perceptual dominance for this percept (63.3% vs. 51.0%, $F(1, 10) = 7.9$, $p = 0.02$). Holding the face percept decreased the perceptual dominance of the house percept (37.9% vs. 51.0%, $F(1, 10) = 8.1$, $p = 0.02$). As for the other stimuli, we found no significant difference in perceptual dominance between the natural condition and the speed-up condition. The bottom panel of Fig. 3c shows that subjects seem to hold both the house and the face by bringing down the number of flips to the alternative percept. The number of flips increased for the speed-up task. Fig. 3d shows that holding the bottom view percept of the Necker cube significantly increases the perceptual dominance for this percept (64.1% vs. 46.4%, $F(1, 10) = 7.9$, $p = 0.02$). Holding the top view percept decreased the perceptual dominance of the bottom view percept (26.3% vs. 46.4%, $F(1, 10) = 8.1$, $p = 0.02$). We found no significant difference in perceptual dominance between the natural task and the speed-up task. Although for the slant rivalry stimulus subjects seem to have a larger control over the number of flips than for the Necker cube, in terms of percept dominance voluntary control plays a similar role for both stimuli. Table 1 presents the disparity percept dominances for the individual subjects for the different rivalry stimuli.

Fig. 4b–d compare the mean percept durations for the orthogonal grating rivalry, the house-face rivalry, and the Necker cube rivalry, respectively. For the orthogonal grating percept duration we found 2.1 s for the natural task, which compares well with the values reported in the literature that range from 1.8 s to 2.4 s (Alexander, 1951; Cogan & Goldstein, 1967; Lack, 1969; Lehky, 1995; Logothetis, Leopold, & Sheinberg, 1996; Meredith & Meredith, 1962; Ross & Ma-Wyatt, 2003). We found that the influence of voluntary control for the different control-exertion tasks for both the left obliques (top panel) and the right obliques (bottom pa-

nel) percept durations was not significant (Fig. 4b). This is consonant with earlier work (George, 1936). A significant effect of voluntary control for the grating stimulus has, however, been reported with different binocular rivalry stimuli (Collyer & Bevan, 1970; Meredith & Meredith, 1962) and a significant control-exertion can be learned (Lack, 1978). Fig. 4c presents the means for the different control-exertion tasks for both the house (top panel) and the face (bottom panel) percept durations. For the natural task we found a percept duration of 3.3 s. In support, Tong reported that the durations for his subjects ranged between 2.5 and 5.5 s (Tong et al., 1998). As for the grating stimulus, we found that the influence of voluntary control on the percept duration was not significant. Fig. 4d portrays the average means for the Necker cube's bottom view (top panel) as well as its top view (bottom panel) percept durations. For the natural task we found a percept duration of 2.7 s (averaged across the two percepts). The literature reports durations in the range between 2.0 and 3.2 s (Babich & Standing, 1981; Peterson & Hochberg, 1983; Ross & Ma-Wyatt, 2003). We found that holding the bottom view percept significantly increased the perceptual duration for this percept (5.0 s vs. 2.6 s, $F(1, 10) = 5.9$, $p = 0.04$). Holding the top view percept significantly increased the perceptual duration for this percept (6.4 vs. 2.8, $F(1, 10) = 7.0$, $p = 0.02$), while decreasing the perceptual duration of the bottom view percept, although not significantly. Finally, attempting to speed-up the perceptual reversals decreased the percept durations for the bottom view (1.7 s vs. 2.6 s) and decreased the durations for the top view (1.9 s vs. 2.8 s). However, this decrease was not significant in both cases. Thus, for the Necker cube we find an influence of voluntary control that is significant for the hold task, and speaking in relative terms, comparable to the slant rivalry. However, in absolute terms the percept durations in the Necker cube stimulus are about 2.5 times shorter than for the slant stimulus. In Fig. 4b–d the black bars are always equally long in the top and the bottom panels. The same is true for the white bars, reflecting a symmetry for the two rivalling interpretations (i.e. house vs. face, or top vs. bottom). Table 2 presents the percept durations for the individual subjects for the different rivalry paradigms.

4. General discussion

In this paper, and in previous work (van Ee, 2002; van Ee et al., 2003), we have compared a variety of temporal aspects of voluntary control across different stimuli for bi-stable perception. It is clear that voluntary control influences the dynamics of perceptual reversals in a quantifiable way and the slant rivalry paradigm seems an especially useful method to study this phenomenon. In comparison to other rivalry paradigms slant

rivalry exhibits beneficial temporal aspects: (1) relatively long percept durations; (2) a clear role of voluntary control in modifying the percept durations. Moreover, slant rivalry has the ability—without changing monocularly visible aspects of the stimulus (see below)—to alter the signals that are responsible for bi-stability in a metrical fashion (pixel-by-pixel, say). The benefits of the metrical aspects for slant rivalry are twofold. First, the perceived surface slant in the voluntarily selected percepts depends on the magnitude of the perspective and disparity signals (van Ee et al., 2003; van Ee et al., 2002). Second, as we have shown elsewhere (Brouwer & van Ee, 2003), the number of perceptual reversals correlates with the conflict between the perspective and disparity signals. We will first discuss each of the mentioned issues.

Why are temporal aspects interesting? Fig. 5 shows the result of a comparison of the strength of voluntary control across the examined paradigms: not only is the percept duration for slant rivalry for the natural control exertion task relatively long, but the increase in duration from the natural to the hold task is also relatively long. For the orthogonal grating stimulus, both the percept durations for the natural task and the increase in duration from the natural to the hold task are relatively short. For studying the role of voluntary control neurophysiologically a significant control over percept durations is sometimes critical. For example, for fMRI studies one needs a sufficient temporal resolution to be able to measure the variations in the blood oxygen level. [5]

Why are metrical (quantitative) aspects interesting? A key feature of the slant rivalry paradigm is that it utilizes the distinction between monocularly and binocularly formed percepts of the 3D layout of a scene. This enables us to modify the disparity-specified slant independently from the perspective-specified slant. In addition, because it is possible to modify the disparity-perspective conflict (that is responsible for bi-stability) without changing monocularly visible aspects of the stimulus one can change the perceived slant or the reversal frequency (or both) such that the subject is not aware of the modifications. Such modifications could be utilized across separate trials, or within a trial. As explained in the methods section, we employed this feature for the catch period (for checking if subjects were not randomly
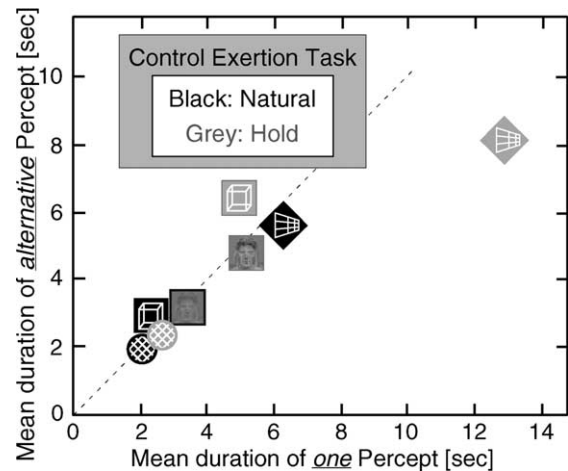

Fig. 5. Voluntary control strength comparison for the four rivalry stimuli. To compare the strength of voluntary control in terms of (changing) percept durations we plotted the natural and the hold durations for the examined paradigms. Along the ordinate we plotted the mean duration (across the six subjects) of one of the two alternative percepts: namely the percept dominated by (1) disparity for slant rivalry, (2) left obliques for grating rivalry, (3) house for house-face rivalry, and (4) bottom view for the Necker cube rivalry. Along the abscissa we plotted the duration of the other of the two alternative percepts: i.e. the percept dominated by (1) perspective, (2) right obliques, (3) face, and (4) top view for the four stimuli, respectively. The black and grey symbols denote the natural and the hold control exertion task for the corresponding percept, respectively. The icons specify the stimuli examined. The slant rivalry stimulus produced the longest percept duration for the natural control exertion task. The increase in duration from the natural to the hold task is also relatively long for the slant rivalry stimulus. For the orthogonal grating stimulus, both the duration for the natural task and the increase in duration from the natural to the hold task are relatively small.

pressing keys). During the catch period disparity and perspective became congruent so that subjects were not aware of (the onset of) the catch period. Another interesting example of a study using a stimulus without changing monocularly visible aspects reports a priming effect for bi-stable stimuli produced by pictures that were pattern masked to prevent conscious representation (Owen, 1985). To our knowledge the extant paradigms do not have the ability to use the monocularly invisible changes for predictable parametric changes in either perceptual reversal, or perceived shape, or both. Metrical aspects may be critically important for neurophysiological experiments: Finding neural activity associated with perceptual reversals, that is causally related to a metrical modification of the disparity-perspective conflict (the variable) of the stimulus—without modifying consciously visible aspects of the stimulus—would be compelling evidence for purely perceptual mediation of the neural activity.

Voluntary control in perceptual bi-stability is clearly limited. Although we can modify the perceptual reversal process, we are often not able to choose the moment of reversal. One could ask whether the term "control" for

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[5] Using the slant rivalry stimulus in an fMRI study, we found correlation between BOLD activation and perceptual reversals towards the disparity-dominated percept in extrastriate cortex. Elsewhere we will present the full results. Concerning the sufficient temporal resolution, the long perceptual durations of the slant rivalry stimulus were helpful but they are not always necessary: Dale has reported that if the time between events is sufficiently randomised (or jittered), events can placed closer in time then the time required for the BOLD signal to return to its baseline (Dale, 1999). However, the time between events does have a lower limit, since the BOLD signal exhibits non-linearities if events are spaced closer then 3 s.

perceptual bi-stability is actually appropriate. Concerning our heart beat rhythm we generally agree that, although we are able to modify it for a limited period of time, we are certainly not able to control it. The term control is generally used for motor actions to describe, for example, hand movements. However, although hand movements are often regarded as being completely voluntary, in fact their control, too, is limited: (1) Many desired movement patterns are impossible when one attempts to move two hands (or eyes) independently of each other; (2) Further, it is for example impossible to draw regular Lissajous figures with voluntarily controlled speed. These limitations in motor control are not mechanically induced but reflect neural processing (review in Rosenbaum, 1991), just as is the case for perceptual control. An interesting proposal is that moving attention from one perceptual interpretation to another might share similar underlying control mechanisms as moving, for example a hand (Leopold & Logothetis, 1999; McDougall, 1906, p. 357).

It is reasonable to state that the disadvantage of the slant rivalry paradigm, certainly relative to binocular rivalry, is that it is not straightforward to teach non-human primates about perspective interpretations because those are inherently cognitive. Nevertheless, successful single cell results have been reported by studies on the perception of perspective-defined slant (Tsutsui, Jiang, Yara, Sakata, & Taira, 2001; Tsutsui, Sakata, Naganuma, & Taira, 2002).

A number of studies in the literature have explicitly focussed on a comparison of the role of voluntary control for the Necker cube and for binocular rivalry (George, 1936; Meredith, 1967; Vernon, 1937; Washburn & Gillette, 1933; see also for discussion McDougall, 1906; Meredith & Meredith, 1962). The results are mixed: some studies reported that control over the Necker cube is large and over binocular rivalry it is very small (George, 1936; Washburn & Gillette, 1933); other studies refute this conclusion (Meredith & Meredith, 1962). According to our results it depends on the aspect that one compares. We found both similarities and differences for the temporal dynamics when we compare the role of voluntary control across the four above-examined paradigms. All stimuli exhibited an increase in the reversal frequency across successive experimental repetitions for the speed-up control exertion task. Our analyses, in which we considered both the perceptual reversal frequency and the dominance periods, provide evidence that for all paradigms the subjects hold either of the two possible percepts by delaying reversals to the alternative percept. Note that, in one of the first systematic studies on voluntary control, Breese stated: "*Each subject was able to increase the length of time a field was seen by fixing the attention upon it. But the number of fluctuations in the rivalry could not be controlled*" (Breese, 1899, p. 25)—our results, thus, do not support

Breese's pioneering work. Further, all of the paradigms showed a drift in the number of reversals across successive 35-s data portions, particularly for the speed-up control task. The similar temporal aspects of the different rivalry paradigms have inspired researchers to propose that binocular rivalry and figural rivalry share common mechanisms (Leopold & Logothetis, 1999; Logothetis et al., 1996; McDougall, 1906; Pettigrew, 2001; Walker, 1975). However, the details of such a mechanisms have not yet been resolved (Blake & Logothetis, 2002; Tong, 2001). Wilson reported evidence that binocular rivalry involves multiple distinct stages (Wilson, 2003). Indeed, instead of looking at the similarities across the different ambiguous stimuli one could also look at the differences. It is for example clear that slant rivalry is under better voluntary control than grating rivalry (our Fig. 5; see also George, 1936; Washburn & Gillette, 1933). It has also been reported that voluntary control over the Necker cube is more affected by drugs (caffeine and sodium amytal) than is binocular rivalry (George, 1936). George stated that "Necker cube alternation involves higher cognitive abilities" than does binocular rivalry, which is "a lower level function".[6] In support, voluntary control over meaningful figures seems to be even more effective than for the Necker cube (Strüber & Stadler, 1999). Although on an operational level the temporal dynamics of the different ambiguous stimuli are clearly different, it cannot be ruled out that there is a, more evolutionary primitive, underlying bistable oscillator process (Pettigrew, 2001) that mediates the reversal process.

What do subjects mentally do when they attempt to voluntarily substitute one percept for another? We have studied the role of both binocular eye movements and blinks while subjects experience bi-stability for our slant rivalry stimulus. Our analyses included micro saccades

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[6] After completion of this paper we learned about a recent useful paper (Meng & Tong, in press). They reported an increase of the dominance duration from the natural to the hold condition of 5% for the grating, 12% for house-face rivalry, and 38% for the Necker cube: in terms of increase proportions 1.0 (grating):2.4 (house-face):7.6 (Necker cube). We found 1.0 (grating):2.2 (house-face):7.9 (Necker cube). We excluded LW from this analysis because his duration for the hold condition of the house percept was three times as long as the mean for the other five subjects (Table 2). Thus, the results from the two laboratories are similar. However, there is also a discrepancy: Our observers have more control (35%) over the house-face percept dominance durations than theirs (12%). There are two clear methodological differences. They used relatively large stimulus sizes for the house face patches (4.2°), and they asked subjects to report blending (which happened 45% of the time). To prevent blending we used the same small size (1.2°) for all stimuli. Because they used different sizes for their stimuli it is hard to directly compare the results. To replicate their findings we have presented our subjects with 4.2° house-face patches, and we also asked our subjects to report the blend percepts. In agreement, we found blending for about 50% of the time, and only about 18% voluntary control. It is an open question whether it is the large stimulus size or the blending that causes less voluntary control.

as small as 5′. The cardinal conclusion for the current paper is that (micro)saccades, blinks and vergence in depth are not essential to voluntarily reverse from one percept to the other. Other studies in which different ambiguous stimuli were presented as afterimages, or stabilized on the retina (Blake, Fox, & McIntyre, 1971), or studies that presented multiple ambiguous stimuli in the visual field, have reported a similar conclusion (review in Leopold & Logothetis, 1999). Intriguingly, we found that both blinks and saccades—but not micro-saccades—are inhibited while subjects make perceptual reversals. An analysis of the eye movement data will be presented elsewhere (van Dam & van Ee, submitted for publication; for an abstract version: van Dam & van Ee, 2003). Another difficult question is what do subjects have to do to delay spontaneous perceptual reversals? One extreme form of the hold condition, up to an almost "stand still" of the percept, has recently been developed into a scientific research tool by Leopold, Logothetis and colleagues (Leopold, Wilke, Maier, & Logothetis, 2002; Maier, Wilke, Logothetis, & Leopold, 2003). They alternated stimulus presentations with blanks to produce the decrease in reversal frequency. The authors proposed a memory explanation that assumes that the percept that just became stored in memory is more easily accessible than an alternative percept. Such an explanation places other accounts in an overarching framework: these accounts include slow down of the reversal frequency under (1) interrupted presentation (Orbach, Ehrlich, & Heath, 1963; Orbach, Ehrlich, & Vainstein, 1963; see also Long & Olszewski, 1999; McDougall, 1906, p. 347; who cites old German literature), (2) displacement (Blake, Sobel, & Gilroy, 2003), or (3) rapid rotation (Brigner & Deni, 1992), as well as suggestions on the involvement of memory (McDougall, 1903, 1906, p. 336). Moreover, the authors reported that the stabilizing effect hinges on perceptual disappearance rather than on actual removal of the stimulus.

We finally speculate on a beneficial role of voluntary control for studying visual awareness. The line of reasoning is the following: Our paper demonstrates that there appear to be clear differences between spontaneous, and voluntarily controlled perceptual reversal processing. In other words, neural activation associated with states of awareness can be examined with or without being accompanied by voluntary control. Note again that using slant rivalry we can modify the level of conflict between the two percepts by changing the disparity- and/or perspective-defined slants without the subject being aware of this modification. Alternatively, one could consider the perceptual reversals that are being instigated by, for example, the Necker cube rivalry and slant rivalry. It would be intriguing to find states of awareness, that show common elements of activity irrespective as to whether the Necker cube or the slant stimulus is being viewed. So far, few neurophysiological contributions (Kleinsch-midt, Buchel, Zeki, & Frackowiak, 1998) have searched for the common neural activity for perceptual reversal instigated by different stimuli.

If we would understand the phenomenon of *voluntary control* in perceptual bi-stability, we would have a cardinal tool for analysing visual perception. If we could discover the neurophysiological difference between voluntarily controlled and spontaneous perceptual reversals, we would have a potentially interesting distinction in terms of neural correlates. The combination of long percept durations and the metrical benefits of slant rivalry, as well as the clear role of voluntary control in it, seem to make slant rivalry a rigorous tool for the scientific study of visual awareness as a biological phenomenon.

5. Conclusion

The main outcome of our quantitative analyses on voluntary control in perceptual bi-stability is that, in comparison to existing rivalry paradigms, slant rivalry exhibits: (1) relatively long percept durations; (2) a clear role of voluntary control in modifying both the percept durations and the perceptual reversal frequency. These aspects, combined with its metrical aspects, make slant rivalry a useful quantitative tool for studying visual perception. Across all conducted investigations a qualitatively similar pattern of temporal dynamics emerged for the four paradigms. The operational quantitative characteristics of binocular rivalry and perceptual rivalry seem to be different: rivalry between figures is better controllable than binocular rivalry.

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