RESEARCH ARTICLE

Grasping isoluminant stimuli

Urs Kleinholdermann · Volker H. Franz ·
Karl R. Gegenfurtner · Kerstin Stockmeier

Abstract We used a virtual reality setup to let participants grasp discs, which differed in luminance, chromaticity and size. Current theories on perception and action propose a division of labor in the brain into a color proficient perception pathway and a less color-capable action pathway. In this study, we addressed the question whether isoluminant stimuli, which provide only a chromatic but no luminance contrast for action planning, are harder to grasp than stimuli providing luminance contrast or both kinds of contrast. Although we found that grasps of isoluminant stimuli had a slightly steeper slope relating the maximum grip aperture to disc size, all other measures of grip quality were unaffected. Overall, our results do not support the view that isoluminance of stimulus and background impedes the planning of a grasping movement.

Introduction

Current theories on vision divide the visual system into two major pathways (Ungerleider and Mishkin 1982; Milner and Goodale 1995). One of these models distinguishes a

U. Kleinholdermann · V. H. Franz · K. R. Gegenfurtner
Department of Experimental Psychology, University of Giessen,
Giessen, Germany

K. Stockmeier
Max Planck Institute for Biological Cybernetics, Tübingen,
Germany

U. Kleinholdermann (✉)
Justus-Liebig-Universitaet Giessen, FB 06/Abt. Allgemeine
Psychologie, Otto-Behaghel-Strasse 10F, 35394 Giessen,
Germany
e-mail: urs.kleinholdermann@psychol.uni-giessen.de

ventral pathway that is mainly concerned with conscious perception from a dorsal pathway, which is responsible for the development of action plans (Goodale and Milner 1992; Milner and Goodale 1995). Corresponding to the different purposes both pathways are supposed to serve, they receive different parts of the available visual information. The ventral system, responsible for delivering a perseverative percept of objects and their spatial relation to each other, has a low temporal but high spatial resolution and a high sensitivity to chromaticity of visual stimuli. This has been shown in numerous studies in monkeys (Zeki 1973, 1978; Komatsu et al. 1992; Takechi et al. 1997; Huxlin et al. 2000) and humans (Meadows 1974; Damasio et al. 1980; Lueck et al. 1989; Zeki 1990; Hadjikhani et al. 1998; Beauchamp et al. 2000; Wade et al. 2002). This can be understood based on the response characteristics of the cells in area V4, which constitute the main source of input for this visual subsystem (Zeki 1980, 1983; Heywood et al. 1992; Felleman and van Essen 1991). The dorsal system on the other hand, receives its main input from area MT which has only a small number of color sensitive neurons (Saito et al. 1989; Gegenfurtner et al. 1994) and whose cells mainly respond to motion (Dubner and Zeki 1971; Maunsell and van Essen 1983; Maunsell et al. 1990; Born and Bradley 2005). This leads to a lower sensitivity for color and fine spatial resolution compared to the ventral system. Instead, temporal resolution and thus movement sensitivity are better in the dorsal than the ventral pathway.

Since the ventral system is proposed to be the major, if not the exclusive source of our conscious percept of the world (Goodale and Milner 1992; Milner and Goodale 1995), it has been a challenge for researchers to come up with experiments where conscious perception and motor planning are at odds. These experiments rely for example on the sensitivity for certain visual illusions, which are

thought not to influence motor plans, while being perfectly visible to an observer (e.g. Agliotti et al. 1995 but see Franz et al. 2000; Franz 2001; Franz and Gegenfurtner 2008). Another branch of research has dealt with neurological patients showing selective deficits assumed to result from a confined lesion to one or the other pathway (c.f., Milner and Goodale 1995; Himmelbach and Karnath 2005). Currently also the effects of stimulating regions associated with one or the other pathway by means of rTMS are investigated (e.g. Schenk et al. 2005).

In this study, we were interested whether the chromaticity of objects is a sufficient feature to establish motor plans for grasp movements. Because only a small fraction of MT neurons responds to chromatic information, one could suppose that movement planning is impaired when a chromatic difference is all which distinguishes the target of a movement from its background. In this case, the dorsal system either somehow has to deal with the limited information it possesses, which should lead to an impaired movement, or it has to draw upon the information available in the ventral pathway which should delay movement execution. The latter was shown for example by Pisella et al. (1998) who found a longer latency in a perturbed pointing task when color instead of position was the stimulus attribute (but see Brenner and Smeets 2004). If we would find an impaired or delayed movement towards a perceptually clearly visible target, this would be an argument in favor of two distinct channels for movement planning and conscious object perception. If on the other hand, chromatic information is sufficient to plan and execute the movement in a completely normal fashion, this would suggest a more holistic view of the perception/action system or at least the notion that crosstalk between the systems is more profound than is commonly thought. This is also what Gentilucci et al. (2001) suggested when they found a color effect on target size estimates. In their study, they showed that red targets are overestimated and green targets underestimated. This, however, was not only true in a manual size estimation task but also observed in grasping movements, pointing to a general process underlying both, perception and action.

In this study, we therefore assessed the quality of grasp movements towards stimuli, which differed in luminance and chromaticity. Our special interest was on those stimuli, which only had a chromatic contrast to the background while their luminance was equal to it (isoluminant stimuli). We wanted to know if those stimuli, because they are solely defined by a property which is not an optimal input for the dorsal stream, impose a challenge to the motor system or are grasped just as stimuli providing luminance contrast or chromatic and luminance contrast together.

In order to assess the quality of a grip we used several measures which have been shown to be related to the

availability of object information for movement planning. As the main measure of interest, we calculated the maximum grip aperture (MGA). Since in the well-known studies of Jeannerod (1984, 1986), the MGA has proven to be a reliable indicator of size information availability in the visuo-motor system. Usually, one finds a linear relationship between object size and MGA with a slope coefficient of about 0.82 (average slope value in the Smeets and Brenner 1999 review of 35 studies). When the amount of visual information about the object is reduced, the normal reaction of participants is a general increase of MGA. This was found in cases where the object was retinally sampled on a coarser scale because it was presented in the periphery of the visual field (Brown et al. 2005; Schlicht and Schrater 2007). It was also observed when sight onto the object was removed before movement initiation (Wing et al. 1986; Berthier et al. 1996; Franz et al. 2009; Hesse and Franz 2009) or during the movement (Jakobson and Goodale 1991; Franz et al. 2009; Hesse and Franz 2009) such that the movement had to be executed relying on memorized information, which is subject to a rather rapid decay (Hesse and Franz 2009).

In contrast to the clear effect of reducing the amount of visual information on the absolute size of MGA, the linear scaling of MGA to object size usually remains surprisingly unaffected. In the studies of Jakobson and Goodale (1991), Brown et al. (2005) and Franz et al. (2009), scaling remained the same for all conditions, which changed the amount of visual information as can be inferred from missing interactions of those conditions with the factor object size. Hesse and Franz (2009) even addressed the issue directly by statistically testing the slope of the scaling function and found no effect of viewing condition. A significant interaction between viewing condition and object size, however, was found in the study of Berthier et al. (1996). Here, the authors used a full vision condition, a reduced vision condition where the target object was glowing in an otherwise dark room and a condition without vision where subjects blindly grasped towards an object, which was previewed before the trial but whose position was only indicated by a sound during the actual grasp trial. In this study, the slope got shallower for the conditions where visual information is reduced. This result though should be interpreted cautiously since the main source of the interaction effect seems to originate from two objects which were unusually small (4 and 9 mm) compared to sizes used in the abovementioned studies (ranging between 20 and 50 mm) which are more representative for the literature on precision grip grasping.

Another important indicator of grip quality is the time of MGA occurence. Smeets and Brenner (1999) report in their review that MGA most often can be found in the last third of the movement. They also show that the timing of MGA

depends on target size (see also Schettino et al. 2003). Furthermore, Weir et al. (1991) discovered that the relative time of MGA is earlier for objects with more slippery surfaces. These findings indicate that grasps which are more difficult may have an earlier occurence of MGA. We would therefore expect that a target, which is less visible to the motor system, would also elicit such a change in MGA timing.

There are two more temporal markers that have been shown to be sensitive to diminished information about the target object of a grasp movement: the movement time (MT), which gets longer (Schettino et al. 2003), and the reaction time (RT) from trial onset to start of the grip (see for example Mon-Williams et al. 2001). Both measures should be prolonged if the motor system is forced to rely on degraded or delayed information.

As the last indicator of grip quality, we assessed the variance of the trajectory. We hypothesized that this variance should increase in conditions with less availability of object information to the dorsal stream.

In order to compare possible effects occurring in the motor domain with the perceptual domain, we also subjected our participants to a perceptual task. Here, we asked them to perform size estimates of our stimuli.

Methods

Participants

We measured ten participants on three occasions. All participants were right-handed (Edinburgh Inventory, Oldfield 1971) without color deficiencies (Ishihara 1995) and naïve to the purpose of the experiment. The age average of the sample was 28 years. Half of the participants were female. For their participation, participants were rewarded with eight euro per hour.

Stimuli

Our stimuli were discs of three different diameters (30, 35, 40 mm) and 13 different colors. The discs were displayed on a computer monitor and seen via a mirror (see the description of the setup below). The set embodied ten discs of green chromaticity (CIE: $x = 0.281$, $y = 0.583$). One of these discs was isoluminant with the background according to the CIE standard observer (photometric isoluminance). In order to deal with the natural variability in individual isoluminance between observers, another green disc was made individually isoluminant for the participant by means of heterochromatic flicker-photometry (subjective isoluminance). The luminance contrast of this disc with the background therefore varied in a range between +1.8 and +10.9% ($\bar{x} = 6.5\%$, $\sigma = 2.8\%$). The luminance of the remaining eight green discs was varied around photometric isoluminance (−8, −4, −2, −1, +1, +2, +4, +8 percent of luminance contrast with the background) in order to assess effects which may occur around the point of isoluminance.

In addition, we presented three achromatic discs, two above (+3 and +43 percent) and one below (−12 percent) the luminance of the background which was at 25 cd/m^2.

In the grasp task, aluminium discs of 5 mm height matched up with the perceived position and diameter of the projected discs. In the perceptual task, the standard disc which was used as a comparison was always achromatic and bright (143% of background luminance).

Setup

Participants were seated in front of a virtual-reality setup, which consisted of a monitor/mirror projection system and the table where our target discs for grasping were placed upon (Fig. 1). The monitor image was projected onto the mirror and produced a virtual image of the display. Distances and angles between monitor, mirror and the table under the mirror were chosen such that the virtual image when looked at was perceived being at the height of the table surface. When a stimulus was displayed on the
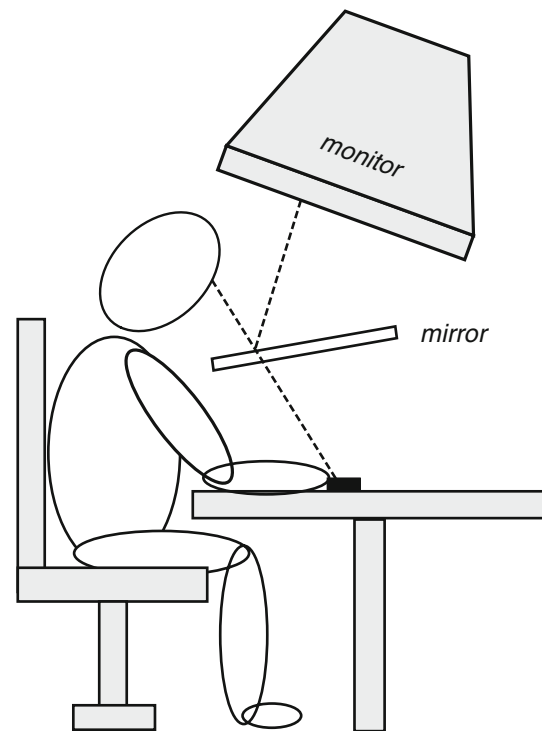

Fig. 1 Experimental setup. Participants looked into a mirror which reflected the image of the monitor. Distances and angles were chosen in a way that the perceived surface was at the height of the table onto which discs in the grasp task were placed

monitor participants, who sat in front of the mirror there-fore perceived the stimulus to lie on the table in front of them. In our grasp task, we positioned the real target disc at exactly the position where the virtual disc image was congruent with it. The perceived distance of the stimuli was then at about 50 cm from the participants eye.

Grasp movements were recorded with an Optotrak 3020 infrared tracking system at a sampling rate of 100 Hz. Three infrared markers were attached to the nails of the index finger and thumb. Using three markers per digit allowed for measuring the touch points on the participants pad surfaces in relation to those markers. At the same time, the pad surfaces stayed free for the grip, allowing full tactile feedback.

The perceptual size estimates and the heterochromatic flicker isoluminance values were collected on the same setup with a computer mouse.

Procedure

In the first experimental session, we determined the indi-vidual point of isoluminance for the participant by means of flicker-photometry (c.f. Kaiser and Boynton 1996): a green target disc was flickered with a frequency of 15 Hz on a background of the same gray as was used later in the experiment. Participants adjusted the luminance of the disc from a random start point until the perception of flicker was minimized or vanished totally. The average luminance value of 15 trials (three disc sizes × five trials) was used to determine the subjective point of isoluminance.

For measuring the grasp movements, participants sat in front of the mirror setup and looked at the virtual surface produced by monitor and mirror. Prior to each trial, the experimenter placed the aluminium disc, which corre-sponded to the presented virtual disc onto a small plastic pin, which served as a mount for the disc. The trial started as soon as the image of the virtual disc was projected onto the gray background. Participants then had 4-s time to grasp the disc with a precision grip of index finger and thumb and transport it to a goal area. After the grasp par-ticipants moved the fingers back to the starting point, a small pin affixed to the experimental table, and the next trial was prepared. All movements were made under open loop conditions, that is no visual feedback of hand or finger position was provided because the digits were obscured by the mirror. The projected target disc image was visible from the beginning of the trial until the real disc was grasped and lifted 20 mm. In each of the three experi-mental sessions, participants grasped every size/color combination three times which makes 117 grasps per ses-sion and 351 grasp trials for every participant in total.

In the perceptual task, participants had to match the radius of the target disc to a standard disc of 30, 35 or 40 mm diameter. The initial diameter was randomly cho-sen between 25 and 45 mm in steps of 1 mm. The target appeared either to the left or to the right of the standard disc. The diameter adjustment was made in 0.2 mm steps by hitting the left and right buttons of a computer mouse. Participants could take as much time as they wanted for the adjustment. When the adjustment was finished, participants hit the center mouse button and the next target/standard pair appeared. In each session, participants adjusted every size/color combination two times which resulted in 78 trials per session and 234 trials total per participant across all three sessions.

In each experimental session, there was one block for the perception task and one for grasping. The order of blocks was reversed in the next session and counterbal-anced between participants.

Results

Grasp parameters

Figure 2 shows the mean MGA for the different disc colors and disc sizes. While there was a clear effect of disc size on MGA, the effect of disc color was nonsignificant as was the interaction. Thus, the absolute size of MGA was not affected by changing the color of stimuli.

The slopes of MGA as a function of disc size in the different color conditions are shown in Fig. 3. We calcu-lated a least square linear regression of MGA on disc size
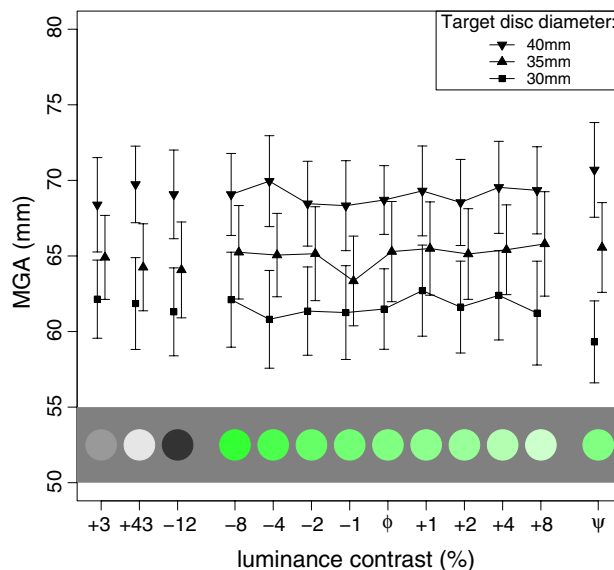

Fig. 2 Mean MGA for different disc sizes and color conditions. Values on the abscissa depict the luminance contrast with the background in percent. ϕ: photometric isoluminance. ψ: subjective isoluminance. *Error bars* are ±1 standard error of the mean (between subjects)
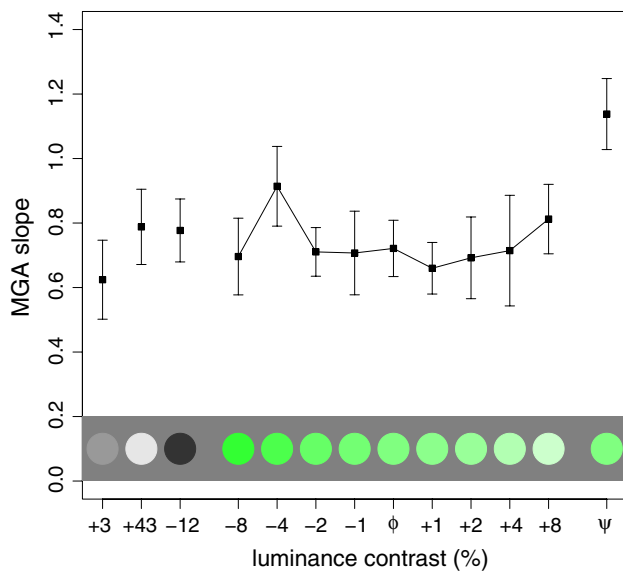
Fig. 3 Mean slope of MGA in the different color conditions. Values on the abscissa depict the luminance contrast with the background in percent. ϕ: photometric isoluminance. ψ: subjective isoluminance. *Error bars* are ± 1 standard error of the mean (between subjects)

for each participant and computed a repeated measures ANOVA of the slope coefficients. There was a main effect of disc color (see Table 1 for all F values). Fisher LSD adjusted post hoc tests revealed significant different slopes between the subjective isoluminant condition and all other color conditions (all $P < 0.05$) except for the green discs with -4 and $+8$ percent deviance from background luminance. The overall slope of MGA on disc size across all participants and color conditions was 0.77.

All temporal measures of the grip were unaffected by variations of disc size and color as can be seen in Table 1. Mean RT was at 394 ms ($\sigma = 133$ ms), mean MT at 788 ms ($\sigma = 255$ ms) and mean time of MGA at 449 ms ($\sigma = 137$ ms).

The analysis of our last movement-quality measure, the movement variance, also showed no effect of disc size or color on the movement.

Perceptual size estimates

The data of perceptual size estimates are shown in Figs. 4 and 5. The ANOVA revealed significant main effects for

Table 1 Results of repeated measure ANOVAs

Measure	Mean	SE	Factor	df_1	df_2	F	P
MGA	65 mm	2.875	Size	2	18	99	<0.001***
			Color	12	108	0.96	0.49
			Interaction	24	216	1.2	0.24
Slope of MGA[a]	0.766	0.069	Size	–	–	–	–
			Color	12	108	1.9	0.038*
			Interaction	–	–	–	–
Time of MGA	449 ms	31.448	Size	2	18	1.6	0.23
			Color	12	108	0.79	0.66
			Interaction	24	216	1.1	0.35
MT	788 ms	51.497	Size	2	18	2.9	0.079
			Color	12	108	1	0.41
			Interaction	24	216	1.3	0.15
RT	394 ms	18.717	Size	2	18	2.1	0.15
			Color	12	108	1.4	0.17
			Interaction	24	216	0.95	0.54
Finger variance	150 mm^2	14.149	Size	2	18	0.68	0.52
			Color	12	108	0.65	0.79
			Interaction	24	216	1	0.45
Thumb variance	138 mm^2	12.963	Size	2	18	0.49	0.62
			Color	12	108	0.67	0.78
			Interaction	24	216	1	0.43
Perceptual size estimates	34 mm	0.278	Size	2	18	5,847	<0.001***
			Color	12	108	15	<0.001***
			Interaction	24	216	0.55	0.96
Perc. size est. slopes[a]	0.989	0.012	Size	–	–	–	–
			Color	12	108	0.6	0.84
			Interaction	–	–	–	–

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

[a] Because the slopes are calculated across all sizes there is no factor size for them

disc size as well as disc color. The interaction was insignificant. Several Bonferroni adjusted post hoc tests were significant at $P < 0.001$. The complete results can be found in Table 2. Significant comparisons are only found for the achromatic stimuli. Especially, the achromatic stimuli with −12 and +3 percent of background luminance were underestimated compared to the other stimuli.

An ANOVA, which was computed across the individual slopes of the perceptual size estimate as a function of disc size did not reveal any influence of stimulus color (see Table 1; Fig. 5).

Discussion

We examined the influence of color information on the quality of grasp movements. We found that the absolute value of MGA, a measure that has proven to be sensitive to the availability of visual information in the visuo-motor system, is not influenced by changing the color of grasp targets. This is also true if the target is isoluminant with the background. For the perceptually isoluminant targets, the ones for which the point of isoluminance was determined with flicker photometry, the slope of the MGA related to target size was significantly higher than for most other targets. This finding might hint to a different processing of these stimuli when the movement plan ist made by the brain. The result though is not in accordance with what one would expect if there were less size information about the
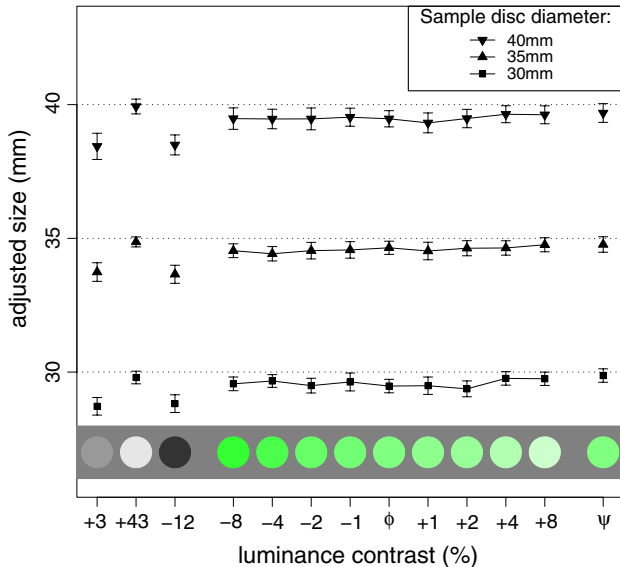

Fig. 4 Estimated disc size as a function of disc color for different disc sizes. Values on the abscissa depict the luminance contrast with the background in percent. ϕ: photometric isoluminance. ψ: subjective isoluminance. *Error bars* are ±1 standard error of the mean (between subjects)
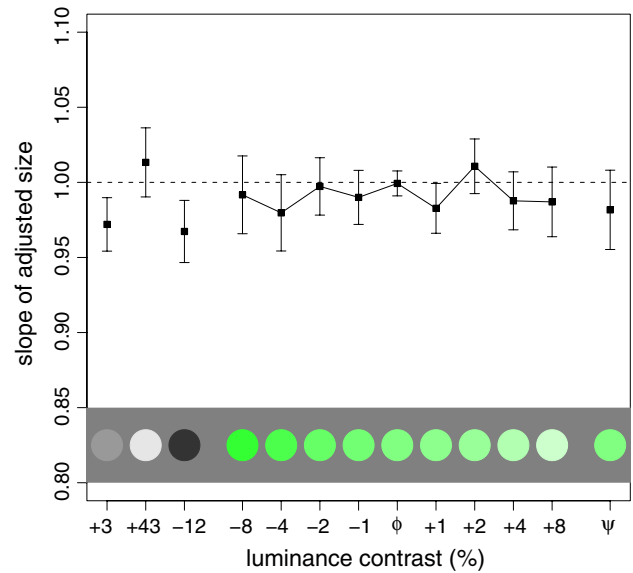
Fig. 5 Mean slope of adjusted disc size in the different color conditions. Values on the *abscissa* depict the luminance contrast with the background in percent. ϕ: photometric isoluminance. ψ: subjective isoluminance. *Error bars* are ±1 standard error of the mean (between subjects). The *dashed line* represents unity scaling

target available in the motor system. In this case, the slope of MGA should rather decrease than increase with a concomitant increase of the average MGA: participants are unsure how large the object is and produce the same very wide opening of their digits in each trial to cover all possible object sizes. This is also what Berthier et al. (1996) found in the only study with significant effects of viewing condition on MGA slope we are aware of. Here, however, we found an increased slope with constant average MGA. Although with a value of 1.14 the slope for the perceptually isoluminant targets comes even closer to a physically perfect scaling than do the slopes found in most other conditions we also do not think that size information obtained from isoluminant targets is more veridical. Such an effect should also be seen in the perceptual data, which was not the case in our study.

All other measures of grip quality did not show significant differences between the isoluminant targets and the other ones. Neither MT, RT, the timing of MGA nor the variance in the movement path were affected by the color of target stimuli. Our findings are in line with the results of White et al. (2006) who found no differences in movement accuracy and latency between isoluminant and non-isoluminant targets as did Anderson and Yamagishi (2000) and Braun et al. (2008). White et al. (2006) also critically reviewed earlier studies reporting longer latencies for isoluminant stimuli in a reaction-time task involving button presses (Burr et al. 1998; Schwartz 1992) or saccades (Perron and Hallett 1995; Satgunam and Fogt 2005; van Asten et al. 1988). Isoluminant stimuli thus do not seem to

Table 2 Perception post hoc test *P* Values

	+3	+43	−2	−8	−4	−2	−1	φ	+1	+2	+4	+8
+43	<0.001***	–	–	–	–	–	–	–	–	–	–	–
−12	0.826	<0.001***	–	–	–	–	–	–	–	–	–	–
−8	0.002	0.010	<0.001***	–	–	–	–	–	–	–	–	–
−4	0.003	0.008	<0.001***	0.892		–	–	–	–	–	–	–
−2	0.001	0.048	<0.001***	0.828	0.869	–	–	–	–	–	–	–
−1	0.004	0.109	0.001	0.582	0.476	0.525	–	–	–	–	–	–
φ	0.002	0.001	<0.001***	0.925	0.859	0.807	0.696	–	–	–	–	–
+1	0.006	0.059	0.003	0.625	0.669	0.590	0.438	0.605	–	–	–	–
+2	0.003	0.009	0.001	0.722	0.832	0.966	0.527	0.634	0.751	–	–	–
+4	<0.001***	0.107	<0.001***	0.088	0.088	0.103	0.357	0.044	0.159	0.015	–	–
+8	0.001	0.193	<0.001***	0.017	0.029	0.056	0.191	0.052	0.056	0.047	0.762	–
ψ	<0.001***	0.501	<0.001***	0.056	0.036	0.033	0.122	0.033	0.027	0.022	0.345	0.544

Row and column numbering indicates the luminance contrast with the background in percent

ϕ: Isoluminance for the CIE standard observer. ψ: subjective isoluminance

* $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$, Bonferroni adjusted

generally delay motoric responses although Braun et al. (2008) recently reported such a delay for smooth pursuit eye movements on isoluminant targets.

On assessing the perceptual size estimates, we found that the two achromatic stimuli with +3 and −12 percent of background luminance led to smaller size estimates than many of the other. It is known that size perception may depend on the luminance of a stimulus especially for low-contrast stimuli (Kulikowski 1975; Gelb and Wilson 1983; Georgeson 1985; Davis et al. 1986). The fact that the smaller estimated disc size for two of the achromatic conditions was not reflected by a smaller MGA in the grasp task is most likely due to the larger variability of the measure than due to a different processing of stimuli in grasping and in perception.

In summary, we conclude that the quality of grasp movements is not profoundly affected by isoluminance of target and background. Since also the finding of a steeper MGA slope in the subjective isoluminance condition does not point to a diminished amount of size information one has to assume that targets solely defined by a chromatic contrast are as suitable for movement planning as targets having a luminance or a luminance and chromatic contrast.

References

Aglioti S, DeSouza JF, Goodale MA (1995) Size-contrast illusions deceive the eye but not the hand. Curr Biol 5(6):679–685

Anderson SJ, Yamagishi N (2000) Spatial localization of colour and luminance stimuli in human peripheral vision. Vis Res 40(7):759–771

Beauchamp MS, Haxby JV, Rosen AC, DeYoe EA (2000) A functional MRI case study of acquired cerebral dyschromatopsia. Neuropsychologia 38(8):1170–1179

Berthier N, Clifton R, Gullapalli V, McCall D, Robin D (1996) Visual information and object size in the control of reaching. J Mot Behav 28(3):187–197

Born RT, Bradley DC (2005) Structure and function of visual area MT. Annu Rev Neurosci 28:157–189

Braun DI, Mennie N, Rasche C, Schütz AC, Hawken MJ, Gegenfurtner KR (2008) Smooth pursuit eye movements to isoluminant targets. J Neurophysiol 100:1287–1300

Brenner E, Smeets JBJ (2004) Colour vision can contribute to fast corrections of arm movements. Exp Brain Res 158(3):302–307

Brown LE, Halpert BA, Goodale MA (2005) Peripheral vision for perception and action. Exp Brain Res 165(1):97–106

Burr DC, Fiorentini A, Morrone C (1998) Reaction time to motion onset of luminance and chromatic gratings is determined by perceived speed. Vis Res 38(23):3681–3690

Damasio A, Yamada T, Damasio H, Corbett J, McKee J (1980) Central achromatopsia: behavioral, anatomic, and physiologic aspects. Neurology 30(10):1064–1071

Davis ET, Kramer P, Yager D (1986) Shifts in perceived spatial frequency of low-contrast stimuli: data and theory. J Opt Soc Am 3(8):1189–1202

Dubner R, Zeki SM (1971) Response properties and receptive fields of cells in an anatomically defined region of the superior temporal sulcus in the monkey. Brain Res 35(2):528–532

Felleman DJ, van Essen DC (1991) Distributed hierarchical processing in the primate cerebral cortex. Cereb Cortex 1(1):1–47

Franz VH (2001) Action does not resist visual illusions. Trends Cogn Sci 5(11):457–459

Franz VH, Gegenfurtner KR (2008) Grasping visual illusions: consistent data and no dissociation. Cogn Neuropsychol 25(7):920–950

Franz VH, Gegenfurtner KR, Bülthoff HH, Fahle M (2000) Grasping visual illusions: no evidence for a dissociation between perception and action. Psychol Sci 11(1):20–25

Franz VH, Hesse C, Kollath S (2009) Visual illusions, delayed grasping, and memory: no shift from dorsal to ventral control. Neuropsychologia 47:1518–1531

Gegenfurtner KR, Kiper DC, Beusmans JM, Carandini M, Zaidi Q, Movshon JA (1994) Chromatic properties of neurons in macaque MT. Vis Neurosci 11(3):455–466

Gelb DJ, Wilson HR (1983) Shifts in perceived size as a function of contrast and temporal modulation. Vis Res 23(1):71–82

Gentilucci M, Benuzzi F, Bertolani L, Gangitano M (2001) Visual illusions and the control of children arm movements. Neuropsychologia 39(2):132–139

Georgeson MA (1985) Apparent spatial frequency and contrast of gratings: separate effects of contrast and duration. Vis Res 25(11):1721–1727

Goodale MA, Milner AD (1992) Separate visual pathways for perception and action. Trends Neurosci 15:97–112

Hadjikhani N, Liu AK, Dale AM, Cavanagh P, Tootell RB (1998) Retinotopy and color sensitivity in human visual cortical area V8. Nat Neurosci 1(3):235–241

Hesse C, Franz VH (2009) Memory mechanisms in grasping. Neuropsychologia 47:1532–1545

Heywood CA, Gadotti A, Cowey A (1992) Cortical area V4 and its role in the perception of color. J Neurosci 12(10):4056–4065

Himmelbach M, Karnath HO (2005) Dorsal and ventral stream interaction: contributions from optic ataxia. J Cogn Neurosci 17(4):632–640

Huxlin KR, Saunders RC, Marchionini D, Pham HA, Merigan WH (2000) Perceptual deficits after lesions of inferotemporal cortex in macaques. Cereb Cortex 10(7):671–683

Ishihara SMD (1995) Ishihara's test for colour-blindness. Tokyo: Kanehara

Jakobson LS, Goodale MA (1991) Factors affecting higher-order movement planning: a kinematic analysis of human prehension. Exp Brain Res 86(1):199–208

Jeannerod M (1984) The timing of natural prehension movements. J Mot Behav 16(3):235–254

Jeannerod M (1986) The formation of finger grip during prehension: A cortically mediated visuomotor pattern. Behav Brain Res 19:99–116

Kaiser PK, Boynton RM (1996) Temporal and spatial factors in color vision. In: Kaiser PK, Boynton RM (eds) Optical Society of America, Washington, pp 357–410

Komatsu H, Ideura Y, Kaji S, Yamane S (1992) Color selectivity of neurons in the inferior temporal cortex of the awake macaque monkey. J Neurosci 12(2):408–424

Kulikowski JJ (1975) Apparent fineness of briefly presented gratings: balance between movement and pattern channels. Vis Res 15(6):673–680

Lueck CJ, Zeki S, Friston KJ, Deiber MP, Cope P, Cunningham VJ et al (1989) The colour centre in the cerebral cortex of man. Nature 340(6232):386–389

Maunsell JH, van Essen DC (1983) Functional properties of neurons in middle temporal visual area of the macaque monkey. I. Selectivity for stimulus direction, speed, and orientation. J Neurophysiol 49(5):1127–1147

Maunsell JH, Nealey TA, DePriest DD (1990) Magnocellular and parvocellular contributions to responses in the middle temporal visual area (MT) of the macaque monkey. J Neurosci 10(10):3323–3334

Meadows JC (1974) Disturbed perception of colours associated with localized cerebral lesions. Brain 97(4):615–632

Milner AD, Goodale MA (1995) The visual brain in action. Oxford University Press, Oxford

Mon-Williams M, Tresilian JR, Bell VE, Coppard VL, Jobling A, Carson RG (2001) The preparation of reach to grasp movements in adults with down syndrome. Hum Mov Sci 20(4–5):587–602

Oldfield RC (1971) The assessment and analysis of handedness: The Edinburgh inventory. Neuropsychologia 9:97–113

Perron C, Hallett PE (1995) Saccades to large coloured targets stepping in open fields. Vis Res 35(2):263–274

Pisella L, Arzi M, Rossetti Y (1998) The timing of color and location processing in the motor context. Exp Brain Res 121(3):270–276

Saito H, Tanaka K, Isono H, Yasuda M, Mikami A (1989) Directionally selective response of cells in the middle temporal area (MT) of the macaque monkey to the movement of equiluminous opponent color stimuli. Exp Brain Res 75(1):1–14

Satgunam P, Fogt N (2005) Saccadic latencies for achromatic and chromatic targets. Vis Res 45(27):3356–3364

Schenk T, Ellison A, Rice N, Milner AD (2005) The role of V5/MT+ in the control of catching movements: an rTMS study. Neuropsychologia 43(2):189–198

Schettino LF, Adamovich SV, Poizner H (2003) Effects of object shape and visual feedback on hand configuration during grasping. Exp Brain Res 151(2):158–166

Schlicht EJ, Schrater PR (2007) Effects of visual uncertainty on grasping movements. Exp Brain Res 182(1):47–57

Schwartz SH (1992) Reaction time distributions and their relationship to the transient/sustained nature of the neural discharge. Vis Res 32(11):2087–2092

Smeets JBJ, Brenner E (1999) A new view on grasping. Motor Control 3:237–271

Takechi H, Onoe H, Shizuno H, Yoshikawa E, Sadato N, Tsukada H et al (1997) Mapping of cortical areas involved in color vision in non-human primates. Neurosci Lett 230(1):17–20

Ungerleider LG, Mishkin M (1982) Two cortical visual systems. In: Ingle DJ, Goodale MA, Mansfield RJW (eds) Analysis of visual behavior. MIT Press, Cambridge, pp 549–586

van Asten WN, Gielen CC, de Winkel ME (1988) The effect of isoluminant and isochromatic stimuli on latency and amplitude of saccades. Vis Res 28(7):827–840

Wade AR, Brewer AA, Rieger JW, Wandell BA (2002) Functional measurements of human ventral occipital cortex: retinotopy and colour. Phil Trans R Soc Ser B 357(1424):963–973

Weir PL, MacKenzie CL, Marteniuk RG, Carboe SL (1991) Is object texture a constraint on human prehension?: Kinematic evidence. J Mot Behav 23:205–210

White BJ, Kerzel D, Gegenfurtner KR (2006) Visually guided movements to color targets. Exp Brain Res 175(1):110–126

Wing AM, Turton A, Fraser C (1986) Grasp size and accuracy of approach in reaching. J Mot Behav 18:245–260

Zeki SM (1973) Colour coding in rhesus monkey prestriate cortex. Brain Res 53(2):422–427

Zeki SM (1978) Functional specialisation in the visual cortex of the rhesus monkey. Nature 274(5670):423–428

Zeki SM (1980) The representation of colours in the cerebral cortex. Nature 284(5755):412–418

Zeki SM (1983) The distribution of wavelength and orientation selective cells in different areas of monkey visual cortex. Proc R Soc Lond B 217(1209):449–470

Zeki SM (1990) A century of cerebral achromatopsia. Brain 113(Pt 6):1721–1777