RESEARCH ARTICLE

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Superior performance for visually guided pointing in the lower visual field

Abstract The superior hemiretina in primates and humans has a greater density of ganglion cells than the inferior hemiretina, suggesting a bias towards processing information in the lower visual field (loVF). In primates, this over-representation of the loVF is also evident at the level of striate and extrastriate cortex. This is particularly true in some of the visual areas constituting the dorsal "action" pathway, such as area V6A. Here we show that visually guided pointing movements with the hand are both faster and more accurate when performed in the loVF when compared to the same movements made in the upper visual field (upVF). This was true despite the fact that the biomechanics of the movements made did not differ across conditions. The loVF advantage for the control of visually guided pointing movements is unlikely to be due to retinal factors and may instead reflect a functional bias for controlling skilled movements in this region of space. Possible neural correlates for this loVF advantage for visually guided pointing are discussed.

Keywords Pointing · Upper/lower visual fields · Dorsal stream · Visuomotor control

Introduction

The dorsal visual pathway, from primary visual cortex (V1) to the posterior parietal lobe, plays a major role in the control of visually guided movements (Anderson 1987; Milner and Goodale 1995). Many of the visual areas in the dorsal pathway of the monkey receive inputs from across the entire retina, including the far periphery. Furthermore, in some dorsal stream regions, such as the parieto-occipital area (PO), the portion of cortex devoted

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to the fovea is no larger than would be expected on the basis of the extent of the visual field it subtends, i.e., there is no "cortical magnification" of central vision (for review see Milner and Goodale 1995). In contrast, the ventral pathway, from V1 to the inferotemporal cortex, receives most of its input from the foveal and parafoveal retina, reflecting its role in object recognition and scene perception (Milner and Goodale 1995). The receptive fields of cells in inferotemporal cortex of the monkey almost always include the fovea and very little of the far periphery (Gross et al. 1971). Evidence from behavioral studies in humans lends support to the idea that there is a differential representation of the visual fields in those brain regions mediating visuomotor control and those mediating our visuoperceptual abilities. It has been demonstrated, for example, that even though people are poor at discriminating between objects of different dimensions appearing in the far periphery, they can nevertheless scale their grip aperture (i.e., the distance between forefinger and thumb) accurately in flight when reaching out to grasp those objects (Goodale and Murphy 1997).

There is some evidence to suggest that differences in visual field representation between the dorsal and ventral streams may also be evident across the upper and lower portions of the visual field. In both humans and monkeys the distribution of ganglion cells across the full extent of the retina is not uniform (Curcio et al. 1987; Curcio and Allen 1990). Beyond the fovea, there is a greater density of ganglion cells in the superior and nasal hemiretinas (Curcio et al. 1987; Curcio and Allen 1990). The density of ganglion cells is approximately 60% greater in the superior hemiretina (Curcio and Allen 1990), suggesting a bias toward the processing of visual stimuli in the lower visual field (loVF). In the monkey, this asymmetry has been shown to persist to the level of the dorsal lateral geniculate nucleus (LGNd) and on into striate and extrastriate cortices (Maunsell and Newsome 1987; Maunsell and Van Essen 1987; Schein and de Monasterio 1987; Galletti et al. 1999). In humans, visual evoked potential and magnetoencephalographic studies have found stronger signals in occipital cortex from loVF stimula-

tion (Fioretto et al. 1995; Portin et al. 1999). Finally, within the dorsal stream itself, single-unit studies in the monkey have demonstrated an over-representation of the loVF in area MT (Maunsell and Van Essen 1987) and in area V6A, an area that has been shown to play a role in the visual control of prehension (Galletti et al. 1999).

If the visuomotor systems in the human brain show a bias towards processing loVF information, then one might expect that such a bias would be evident in skilled movements such as pointing. To test this idea, we used a visually guided pointing task with a well-defined speed-accuracy trade-off function (Fitts 1954; MacKenzie et al. 1987; Decety and Michel 1989; Maruff et al. 1999a, 1999b). The task requires subjects to make *fast* and *accurate* pointing movements to targets of different sizes. Typically, subjects make slower movements to smaller targets, presumably reflecting the increased demands for accuracy with these targets. Therefore, it is possible to explore how subjects trade speed for accuracy in the upper visual field (upVF) and the loVF to investigate possible biases in visuomotor control in these regions of space.

Materials and methods

Subjects

Eight graduate students (five female, three male; mean age= 23.13 years; SD=8.04) participated in this experiment. All subjects were right handed and had normal or corrected to normal visual acuity. Informed consent was obtained from each subject prior to commencing the task and the protocol was approved by the University ethics committee.

Stimuli and procedure

The visually guided pointing task required subjects to make five repetitive pointing movements to targets that vary in size, as quickly and accurately as possible (Fig. 1). Subjects sat with their head comfortably in a chin rest that also stabilized their forehead. Subjects made five pointing movements with their right index finger to targets of different sizes, while fixating a cross in either the upper or lower part of the work space (Fig. 1). When fixating a cross in the upper part of the display, targets and movements were located in the loVF. Conversely, when fixating a cross in the lower part of the display, targets and movements were located in the upVF. Moving the fixation point but not the targets meant that the biomechanical requirements of the movements made in both visual fields were identical. Targets consisted of open squares with sides of 1.9, 3.7, 7.5, 14.9 and 30 mm in length. The centre of each target appeared 3 cm to the right of a vertical line of 8 cm in length. Fixation crosses were placed either 4 cm above or below the vertical line (Fig. 1).

Target stimuli were presented on a sheet of A4 paper that was stabilized on a board. The board was raised at an angle of approximately 30° from the tabletop. The chin rest was tilted forward so that the subject's head was parallel with the plane on which the targets were presented. Therefore, when fixating in either fixation point, targets subtended the same degree of visual angle but appeared in mirror symmetrical positions in the upper and lower visual fields. Calculation of the visual angle subtended by targets was made as if the eyes were focused on a midpoint between the two fixation crosses. At a viewing distance of approximately 30 cm, then, the largest target would have subtended an angle of approximately 5°. Subjects were instructed before beginning the
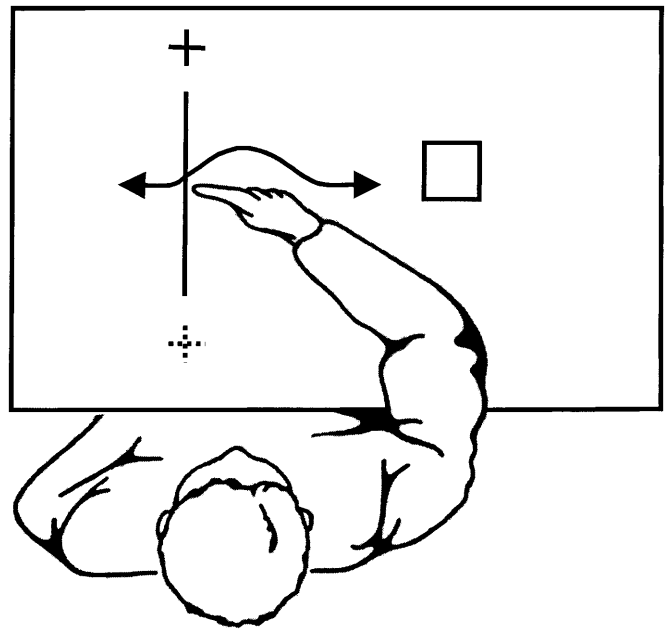

Fig. 1 Schematic representation of the stimulus display. The arrow indicates the directions in which the subject points. Note that when fixating a cross in the upper portion of the display (*solid cross* shown here) movements and targets are located in the loVF, while fixating a cross in the lower portion of the display (*dashed cross* shown here) ensures movements and targets are located in the upVF. Only one cross is present during any given trial. The biomechanics of movements do not differ across conditions and the experimental setup and stimuli were designed such that targets would subtend the same degree of visual angle in each visual field (see Materials and methods)

task to emphasise both speed and accuracy equally. A single trial consisted of the following: subjects were given a verbal signal to commence their movement by the experimenter and began their first movement to the left of the vertical line, always completing their final movement to the left of this line. The five pointing movements were made towards the center of the target and back (Fig. 1). Subjects completed two trials for each of the five targets in both the upVF and the loVF (20 trials in all). Target size and visual field were randomized throughout the task and subjects were given brief rest periods between each trial.

Movement kinematics were measured on line by a three-camera system that monitored infra-red light-emitting diodes (IREDs) placed on the subject's index finger and wrist. Movement onset was defined as the point at which velocity exceeded 5 cm/s for more than ten consecutive time frames, whereas the end of a movement was defined by the absolute trough of the final peak of an individual's velocity profile.

Data analysis

Movement duration

For each subject, mean movement duration (MD) for the two trials for each target in each visual field was calculated. Group means were then calculated and a repeated-measures ANOVA with the factors of visual field and target size was conducted to establish the existence of an interaction between these factors. Least squares regression was then used to model this interaction in the upper and lower visual fields separately. Data for these analyses were organised according to an index of difficulty (ID) as calculated by Fitts' Law (Fitts 1954). Fitts' Law, derived from information theo-

ry, states that MD will be a function of the combination of the amplitude of movements (A) and the width of targets (W), expressed as an index of difficulty (ID) according to the following logarithmic law:

$$ID = \log_2(2\,A\,/\,W)$$

According to Fitts' law, MD should increase linearly with increases in ID. This effect has been shown to be robust, requiring small numbers of subjects and very few trials per subject (Maruff et al. 1999a, 1999b). In addition, a trend line was fitted to each subject's data in each visual field separately, with the values for the slope (a measure of the degree to which MD increases as ID increases) and y-intercept of these equations treated as dependent variables that were compared using paired samples *t*-tests.

Peak velocity

Each individual movement within a trial involved two velocity peaks, one for movements made *towards* the target and a second peak for the *return* movement for a total of ten velocity peaks per trial. As only movements made towards the target included an accuracy requirement (i.e., placing the finger at the center of the target), velocity profiles were first inspected for any differences in the two sets of peaks. In addition, this analysis was used to establish a visual field by target size interaction, as in the analysis for MD. Repeated measures ANOVA with the factors of visual field, target size, and direction of movement, revealed no difference between the peak velocities of movements made towards and away from targets [$F(1,7)=2.2$, $P=0.18$]. Furthermore, the direction of movement did not interact with either visual field or target size. Thus, all further analysis of peak velocity was conducted with data collapsed across movement direction. This was done as the task involves a continuous performance as opposed to discrete single movements. Least squares regression analysis was used to fit linear trends to the data in each visual field to test the hypothesis that peak velocity would increase as target width increased.

Accuracy

Subjects aimed at each target five times per trial. To investigate absolute differences in accuracy, radial displacement (RD) distances were calculated for each movement end point within a trial for each subject separately. Raw endpoint data were corrected for the position of the IRED on the subjects' finger (i.e., while the pad of the subject's finger contacted the target, IREDs were placed on the dorsal portion of the finger, some distance from the point of contact). Radial displacement was calculated by taking the square root of the sum of squared x and y displacements for each end point separately [i.e., $RD=\sqrt{x^2+y^2}$. Mean RD for each trial was calculated for each subject individually with group means being subjected to a two (visual field; upVF versus loVF) by five (target size; 1.9, 3.7, 7.5, 14.9, and 30 mm) repeated measures ANOVA. Main effects and interactions were investigated with paired samples *t*-tests.

Results

Movement duration and peak velocity

For MD, ANOVA indicted a significant visual field by target size interaction [$F(1,7)=9.37$, $P<0.05$]. No other effects were significant. Least squares regression analysis revealed a significant linear trend for MD as a function of target size only for movements made to loVF

Table 1 Least squares regression estimates for linear lines of best fit for group mean data for movement duration and peak velocity; *upVF* upper visual field; *loVF* lower visual field

	Linear equation	r^2
Movement duration as a function of index of difficulty		
upVF	y=4.79x+2.79	0.41
loVF	y=12.8x+2.53	0.90*
Peak velocity as a function of target width		
upVF	y=3.95x+147.31	0.31
loVF	y=16.38x+123.27	0.92*

*Significant at $P<0.01$

targets. In other words, MD increased linearly with ID for movements made to targets in the loVF, while no such relationship was evident for movements made to targets in the upVF (Table 1 and Fig. 2A). Paired samples *t*-tests on the slope for regression lines fitted to each individual's data separately indicated a significant difference [$t(7)=2.41$, $P<0.05$] such that the slope for MD in the loVF was steeper than the slope for MD in the upVF (Fig. 2B). The same analysis for the y-intercept approached significance [$t(7)=2.27$, $P=0.058$], with the mean intercept for loVF movements being lower than the intercept for upVF movements (Fig. 2C).

A similar difference between movements made to upper and lower visual field targets was seen in the functions describing the relationship between target width and peak velocity (Table 1 and Fig. 3). ANOVA indicted a significant field by target size interaction [$F(1,7)=8.43$, $P<0.05$] with no other effects significant. Again, least-squares regression analysis revealed a significant linear relationship between peak velocity and target width for movements made to loVF targets, such that peak velocity increased linearly as target width increased (Fig. 3). The same relationship was not significant for targets appearing in the upVF (Table 1 and Fig. 3).

Accuracy

Repeated-measures ANOVA conducted on mean end point accuracy for the group (i.e., measured as a radial displacement from the target center) indicated a main effect of visual field [$F(4,28)=26.6$, $P<0.01$] that was subsumed by a significant visual field by target size interaction [$F(4,28)=3.57$, $P<0.05$]. As can be seen in Fig. 4, with the exception of the smallest target, the terminal end points were more accurate for targets viewed in the loVF than for targets viewed in the upVF (for target width 3.7 mm, [$t(7)=-3.48$, $P<0.01$; for target width 7.5 mm, $t(7)=-5.57$, $P<0.01$; for target width 14.9 mm, $t(7)=-3.36$, $P<0.01$; for target width 30 mm, $t(7)=-2.52$, $P<0.05$].

Fig. 2 A Group mean (±SD) movement duration (*MD*) plotted against index of difficulty (*ID*) as calculated by Fitts' law (Fitts 1954). Linear lines of best fit are plotted on this figure (*open circles* and *dashed lines* represent upVF targets, while *filled squares* and *solid lines* represent loVF targets; see Table 1 for equations).
B Group mean (±SE) slope as a function of visual field.
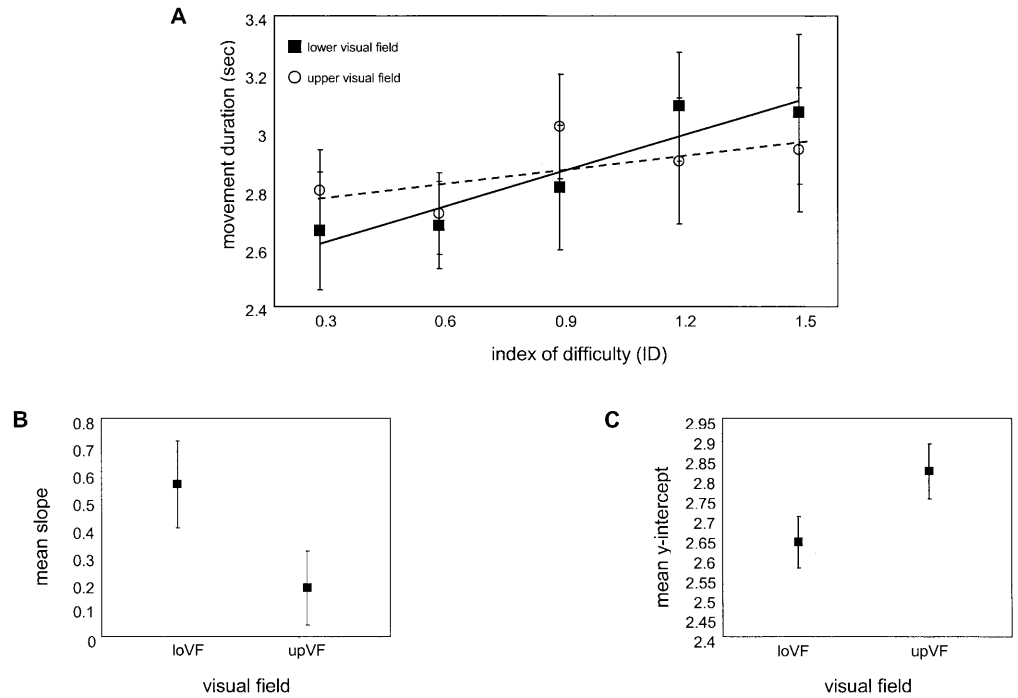**C** Group mean (±SE) y-intercept as a function of visual field

Fig. 3 Group mean (±SE) peak velocity plotted against target size. Linear trend lines are fitted for both upper and lower visual field (symbols are the same as for Fig. 2A; see Table 1 for equations)
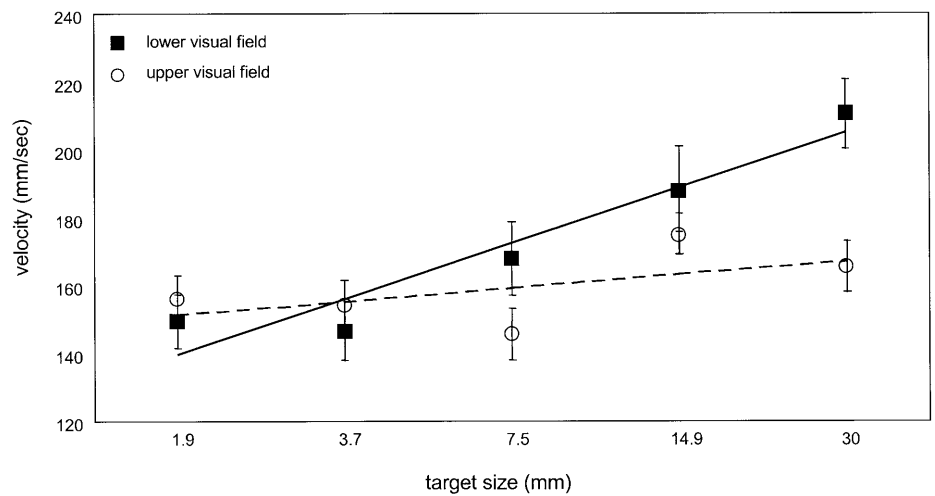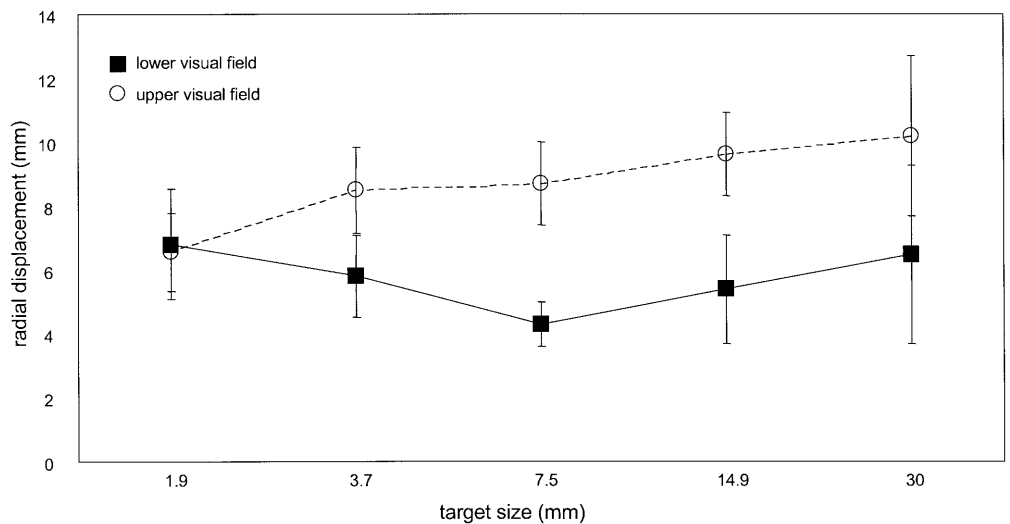

Fig. 4 Group mean (±SE) radial accuracy data plotted at each target size for both the upper (*open circles*, *dashed line*) and lower (*filled squares*, *solid line*) visual fields

Discussion

When subjects viewed targets in their loVF, they demonstrated a clear relationship between target size and speed of movement, with peak velocity of their movements increasing as the target size increased (Fig. 3). The same relationship was not evident when subjects viewed targets in their upVF. Furthermore, movements made to targets in the loVF were more accurate than similar movements made to upVF targets (Fig. 4). Importantly, this shows that overall subjects were not simply sacrificing accuracy for speed in the loVF. This striking difference between performance in the upper and lower visual fields is all the more intriguing given that the biomechanical requirements of the movements were identical in both viewing conditions. Subjects simply shifted their fixation to a point above or below the work space (Fig. 1). By merely shifting fixation so that the pointing finger and target were viewed in the upVF, the well-defined relationship between target size and movement duration as described by Fitts' Law (Fitts 1954), was eliminated. Subjects' subjective experience of this task corresponded well with their overall performance, with most subjects reporting experiencing greater difficulty when making movements in upVF. Given the small degree of visual angle covered by the stimulus display (see Materials and methods section) it is unlikely that the physical differences in fixating in either the upper or lower portion of the display led to this subjective impression of difficulty. Instead, some other aspect of the task requirements for pointing in the upper versus the lower visual field is likely to have contributed to the subjective feeling subjects had that the task was more difficult when movements were made in the upVF. Because we did not monitor eye movements, we cannot be absolutely certain that subjects always complied with instructions to maintain fixation. But if subjects had failed to maintain fixation more often in the upVF and had instead foveated the targets, then this presumably would have reduced any differences in accuracy across the two visual fields. Following the same logic, one would have expected a stronger relationship between movement speed and target size than was observed in the upVF.

It is unlikely that the differences between upper and lower visual field performance are due to any distortion in the perception of the targets in either visual field. Targets subtended the same visual angle in both fields (approximately 5° for the largest target). The fact that targets were located in the near, rather than the far periphery, also argues against an exclusively "retinal" explanation for the observed differences in performance. The asymmetries in retinal ganglion density are seen most dramatically further out into the visual periphery (i.e., around 30° and beyond; Curcio et al. 1987; Curcio and Allen 1990), well beyond where the targets were presented in our study. The superior performance for movements made in the loVF may in fact reflect a bias in processing that continues well into the central visual pathways, particularly in some regions of the dorsal stream, which are thought to play a special role in the visual control of skilled actions (Goodale et al. 1991; Goodale and Milner 1992; Milner and Goodale 1995). As mentioned in the Introduction, a number of dorsal-stream areas in the monkey that show an "over-representation" of the loVF have also been implicated in the visual control of reaching (Galletti et al. 1999).

The loVF advantage that we observed is also consistent with a recent proposal that the loVF is more concerned with processing visual information in peripersonal space, while the upVF is more concerned with processing information in extrapersonal space (Previc 1990, 1998). According to this account, a loVF emphasis on processing of stimuli in peripersonal space reflects its role in the control of actions such as grasping and the manipulation of tools, while the upVF bias towards extrapersonal space reflects its special role in scene parsing, object identification, and visual search (Previc 1998). Results from behavioral studies in humans, using a wide variety of experimental paradigms, are somewhat contradictory on this last point (see Previc 1990, 1998 for a detailed review of the range of upVF advantages found in behavioral studies). Demonstrations of superior perceptual processing (e.g., letter or word recognition and visual search) have been shown for the upVF in some studies and for the loVF in others (Mishkin and Forgays 1952; Heron 1957; He et al. 1996; Carrasco et al. 1998). In addition, it has been claimed by some that any advantage for processing loVF information may actually reflect biases in the way in which visual spatial attention is directed (He et al. 1996), although this point has also been recently disputed (Carrasco et al. 1998). What is clear from the present experiment, however, is that there is a pronounced advantage for controlling visually guided pointing movements when those movements are carried out in the loVF.

In summary, the results of the present study provide support for the notion that the control of skilled, visually guided motor actions is better in the loVF. Indeed, these findings complement the results of several neurophysiological studies in the monkey showing a bias in the representation of the loVF from the thalamus through to visual areas in the dorsal stream (Maunsell and Newsome 1987; Maunsell and Van Essen 1987; Schein and de Monasterio 1987; Galletti et al. 1999). Despite the fact that neuroimaging has been used to investigate the organization of homologous regions in the human brain (Tootell et al. 1998), there has been no systematic investigation of possible biases in the representation of the upper and lower visual field in these structures. Revealing such biases, however, may require more than the usual retinotopy study in which subjects passively view stimuli that are moved systematically through their visual field. Instead, it may be necessary for subjects to perform visually guided tasks that require the subjects to make use of stimuli presented in different parts of the visual field.

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