HUMAN PROSACCADES AND ANTISACCADES UNDER RISK: EFFECTS OF PENALTIES AND REWARDS ON VISUAL SELECTION AND THE VALUE OF ACTIONS

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Abstract—Monkey studies report greater activity in the lateral intraparietal area and more efficient saccades when targets coincide with the location of prior reward cues, even when cue location does not indicate which responses will be rewarded. This suggests that reward can modulate spatial attention and visual selection independent of the "action value" of the motor response. Our goal was first to determine whether reward modulated visual selection similarly in humans, and next, to discover whether reward and penalty differed in effect, if cue effects were greater for cognitively demanding antisaccades, and if financial consequences that were contingent on stimulus location had spatially selective effects. We found that motivational cues reduced all latencies, more for reward than penalty. There was an "inhibition-of-return"-like effect at the location of the cue, but unlike the results in monkeys, cue valence did not modify this effect in prosaccades, and the inhibition-of-return effect was slightly increased rather than decreased in antisaccades. When financial consequences were contingent on target location, locations without reward or penalty consequences lost the benefits seen in noncontingent trials, whereas locations with consequences maintained their gains. We conclude that unlike monkeys, humans show reward effects not on visual selection but on the value of actions. The human saccadic system has both the capacity to enhance responses to multiple locations simultaneously, and the flexibility to focus motivational enhancement only on locations with financial consequences. Reward is more effective than penalty, and both interact with the additional attentional demands of the antisaccade task. © 2010 IBRO. Published by Elsevier Ltd. All rights reserved.

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The influence of anticipated outcome (e.g. reward, penalty) on spatial attention is a key issue in research on decision making and cognitive control (Maunsell, 2004). It is possible that effects of reward and penalty are mediated by attentional systems, for example, through general increases in arousal and motivation (Maunsell, 2004; Hickey et al., 2010). However, there is also evidence that specific striatal dopaminergic processes mediate reward effects, an independent source of modulation as postulated by the incentive-salience hypothesis (Berridge and Robinson, 1998).

A recent study on monkeys showed that reward does enhance visual attention at a cue location (Peck et al., 2009). Monkeys were shown a peripheral cue that indicated whether or not a saccade in that trial would be rewarded. The target for the saccade could appear at the cue's location or on the opposite side: the key point was that a correct response to either would be rewarded. Hence, the cue did not specify a specific action that would be rewarded, as would have been the case if reward occurred only for saccades to targets that appeared at the location of the cue. Despite the fact that reward was not spatially contingent, neurons in the lateral intraparietal area (LIP) showed greater activity when cues in their receptive fields indicated a reward, compared with a non-reward cue. Behaviorally, on non-reward trials, the monkeys were slower to saccade to targets that appeared where the cue had been, suggesting an effect related to "inhibition of return," in which attention is slower to return to recently inspected locations (Posner et al., 1985). However, on rewarded trials, this was reversed, and saccades were more rapid and accurate when the reward cue and the target shared the same location.

This finding differs from prior studies that found that reward can enhance attention at the location to which a specific saccade is to be made, optimizing the efficiency of the motor response, with reward changing the responses of neurons whose receptive fields include the location of the target of the saccade. This is the "action value" hypothesis, in which reward acts to enhance a specific motor action (Platt and Glimcher, 1999; Dorris and Glimcher, 2004; Sugrue et al., 2004). The results from Peck et al. (2009) showed that, while both right and left saccades were rewarded on reward trials—that is, both had equal action value—the saccades to targets located where the cue had been were still faster. Hence, this suggests that reward can modulate visual selection as well as action selection.

The initial aim of the present study was to determine whether motivational cues create similar local spatial attention effects in human saccades. If so, this would provide

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Abbreviation: LIP, lateral intraparietal area.*

evidence that reward interacts with visual spatial attention in humans, by selectively enhancing performance at cue locations, even when those cues do not indicate spatially selective rewarded locations. Next, we aimed to extend these observations in three directions.

First, the previous study examined two cue conditions, one indicating reward (juice delivered) and one its absence (juice not delivered). To more fully understand the effects of motivational valence in humans, we considered not only monetary gain but also monetary loss. Previous studies have been inconsistent regarding whether reward and penalty produce the same modulatory outcome, and there is evidence that these two motivators are mediated by different neural substrates (Matsumoto and Hikosaka, 2007). Hence, in humans, it is important to examine the effect of motivational valence in addition to the effects of reward only.

Second, human studies show that antisaccades—a saccade of the same amplitude but in the direction opposite to a visual target—are more attentionally demanding than prosaccades—a saccade to the visual target—with longer latencies and higher error rates (Munoz and Everling, 2004). If the spatial effect of a motivational cue observed by Peck et al. operates by enhancing attention at the location of the reward cue, then we hypothesize that this modulatory effect may be more apparent in antisaccades than in prosaccades, particularly because prosaccades may already be a fairly optimized response. Indeed, some previous studies of reward on human saccades have found effects on antisaccades but not on prosaccades (Duka and Lupp, 1997; Mueller et al., 2010), though others have found effects on both (Jazbec et al., 2006).

Third, in the study by Peck et al. (2009), the important feature was that the location of the reward cue in relation to the location of the target had no bearing on whether the monkey received a reward. Hence, reward was not contingent on target location. Because of this, selective enhancement of performance when the target coincided with the cue location could not be attributed to action value. However, the design of this study cannot exclude the possibility of additional effects that are indeed generated by action value, in which reward is linked to a specific motor action (Platt and Glimcher, 1999; Dorris and Glimcher, 2004; Sugrue et al., 2004). Hence, our final aim was to examine effects that emerged when reward was made contingent on the relationship between cue location and target location.

EXPERIMENTAL PROCEDURES

Subjects

Sixteen participants with a mean age of 21.8 years (range, 18–27) participated, 10 of whom were male. All were healthy with no prior psychiatric or neurological illness, were not on any medication, had normal or corrected-to-normal visual acuity, and were not color blind. None reported caffeine intake in the 4 h preceding the experiment. Three subjects were occasional smokers, but all smoked less than one pack a week. The institutional review boards of Vancouver General Hospital and the University of British Columbia approved the protocol, and all subjects gave informed consent in accordance with the declaration of Helsinki.

Apparatus and procedure

Subjects sat in standard room lighting, 57 cm away from a 22″ NEC FE2111SB monitor, with their head on a chin rest, viewing with both eyes. Two acoustic speakers were positioned symmetrically facing the subject from atop the monitor. Screen resolution was 1024 by 768 pixels, corresponding to 39° by 30° of visual field. Saccades were recorded from the left eye by an Eyelink 1000 video-based recording system (http://www.sr-research.com, Kanata, Ontario, Canada). Stimuli, trials, and experimental blocks were created using SR Research Experiment Builder 1.1.2.

During this task, participants were instructed to either look toward (prosaccade) or away from (antisaccade) a suddenly appearing visual stimulus. Prosaccade and antisaccade trials were presented in two separate blocks, not mixed. Prior to the appearance of the stimulus, a motivational cue indicating a reward, a penalty, or no consequence (neutral) appeared in one of the two potential stimulus locations. We examined the effects on saccade performance of cue valence (reward, penalty, neutral), the location of the visual target (same or opposite side as the motivational cue), task instruction (prosaccade, antisaccade), and finally contingency (i.e. whether or not the financial consequence depended on the visual target and cue being on the same side). The contingent and noncontingent sessions were conducted on separate days. A condition with no cue also provided a baseline.

Each trial began with a fixation cross at the center of a display with a homogenous gray background (Fig. 1). After the subject had maintained eye position within 1.5° of the cross for 300 ms, a cue appeared for 300 ms at 9.5° eccentricity, either right or left of the cross. Cues were discs of 6.2° diameter. Subjects had to continue maintaining fixation within 1.5° of the fixation cross, which was still visible while the cue was present. There were four different cues signifying different motivational conditions. The reward cue was a green disc with a dollar sign: this indicated that a correct response would earn the subject 25 cents, whereas an incorrect one had no financial consequence. The penalty cue was a red disc containing an "X": this indicated that an incorrect response would cost 25 cents, but a correct response would have no financial consequence. The neutral cue was a blue disc with a wave symbol: this indicated that neither correct nor incorrect responses had financial consequences. Finally, the baseline condition had no cue, and was similar to the neutral condition in that responses had no financial consequences. To control for the possible alerting mechanism of peripheral cues, in the no-cue condition the fixation cross increased in size by 36% during the same 300 ms period that the cue appeared in the other conditions.

After the cue, there was a 600 ms fixation period during which gaze had to be maintained within 1.5° of the still visible fixation cross. At the end of this period, the cross disappeared and a black disc of 1° diameter appeared either right or left at the same eccentricity as the prior cue. Subjects were instructed to make their saccades as quickly as possible. If by 800 ms after disappearance of the fixation cross the subject had not made a saccade that landed in right or left zones of 18.5° diameter surrounding the two potential saccadic goals, the message "Time's up" appeared, and the trial was aborted. These incomplete trials were repeated later in the same block, without the subject being informed of this.

In completed trials, feedback was given only for trials with financial consequences. When the subject won a reward, they saw a picture of a stack of gold coins for 500 ms concurrent with a cash register sound. When they were penalized for making a saccade into the wrong zone, they saw the stack of coins with a thick red line through it, concurrent with an unpleasant buzz (similar to that used on TV game shows to indicate a wrong answer), lasting 500 ms. For trials with no financial consequences, a blank screen appeared for the same duration of 500 ms, with no
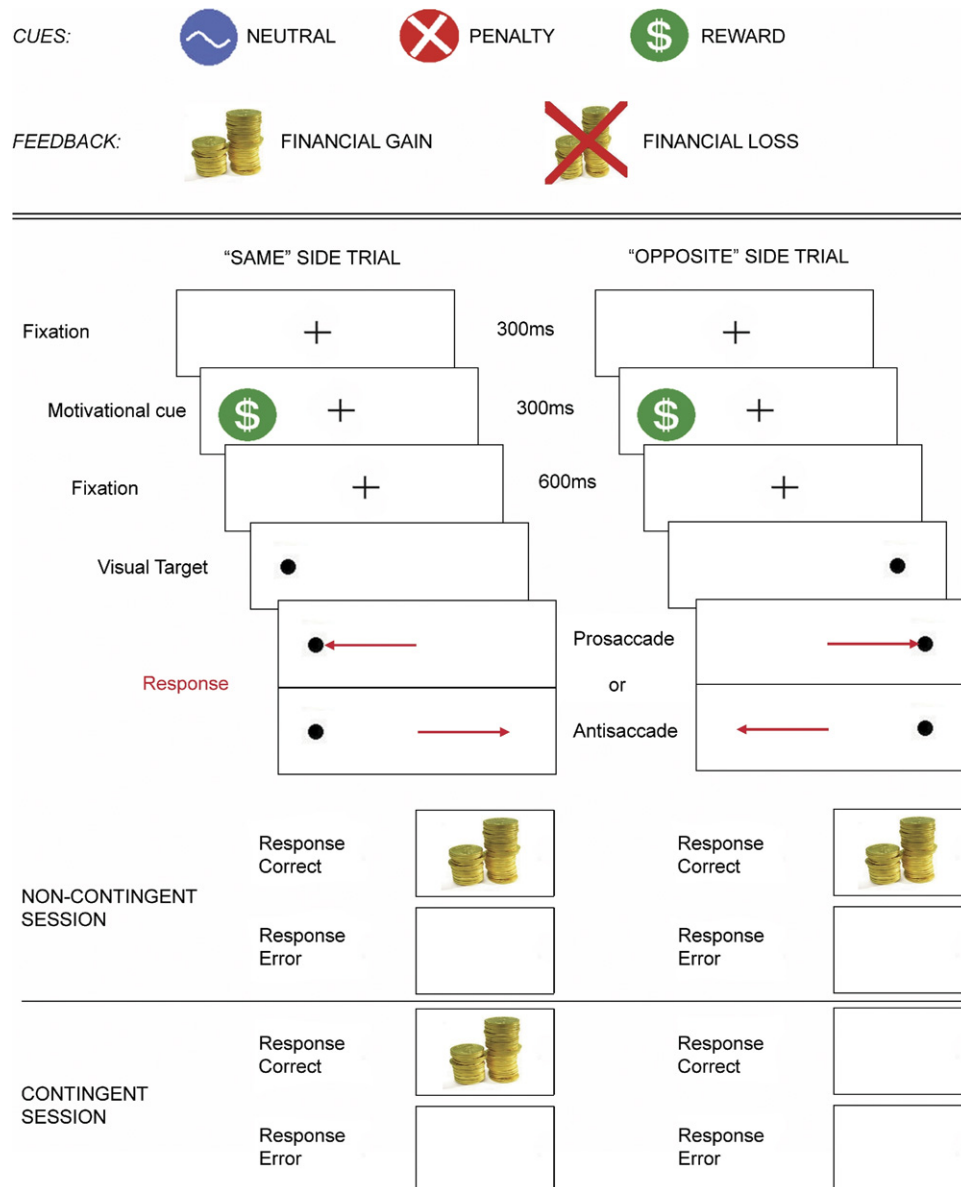
Fig. 1. Experimental procedure. Top shows symbols used as motivational cues in the neutral, penalty, and reward trials, and the symbols used to give feedback when subjects received financial gain for a correct saccade in a reward trial, and when they suffered financial loss for an incorrect saccade in a penalty trial. Below shows an example of the sequence of events in two reward trials varying in visual target/cue congruency, one on the left where the cue and the visual targets are on the "same" side, and one on the right where they are on "opposite" sides. Responses can be either correct or incorrect (red arrows depict direction of correct saccade): correct trials are rewarded in the noncontingent session regardless of visual target/cue congruency, whereas only those with the cue and visual target on the "same-side" are rewarded for prosaccades, and for antisaccade, in the first group of subjects. (In the second group, antisaccades were rewarded in the contingent sessions when the cue and the visual target were on opposite sides.) For errors on these reward trials, nothing appeared on the screen, as subjects suffered neither financial gain nor loss. For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.

sound, regardless of whether the saccade was correct or incorrect.

Each subject performed four blocks of 320 trials, for a total of 1280 trials, in two sessions on two different days, separated by no more than a week. Two blocks were performed per session, one requiring prosaccades and the other antisaccades. Each block contained equal numbers of reward, penalty, neutral and no-cue trials in random order. In the first of the two sessions, the side of cue appearance had no bearing on the financial consequence, as in the prior monkey study (Peck et al., 2009). That is, in this "non-contingent" session, neither reward nor penalty was contin-

gent on whether the stimulus was on the same or opposite side of the motivational cue.

The second of the two sessions examined the effect of making consequences contingent on congruence between the location of the cue and stimulus. The order of sessions was not counterbalanced, to avoid possible carry-over effects between sessions of contingency on responses. For prosaccades, consequences occurred only on trials when the stimulus appeared at the location of the motivational cue. For antisaccades, it was not clear whether contingency would have an impact when the stimulus and the cue were spatially congruent, or when the

saccade and the cue were spatially congruent. Hence, we divided the subjects into two groups that were demographically similar[1]. The first group had an antisaccade contingent block in which financial consequences occurred on trials in which the stimulus appeared at the same location as the motivational cue. The second group had an antisaccade contingent block in which consequences occurred on trials in which the stimulus appeared on the opposite side of the cue.

At the end of the entire experiment, subjects were paid the net amount that they had won in the two sessions, which was on average $68.32 (range, $60–$80).

Analysis

Saccade latency was defined as the interval between visual target onset and saccade onset, which was identified by SR Research Data Viewer 1.7.5 (http://www.sr-research.com) as the time when eye exceeded 35°/s or acceleration exceeded 9500 °/s^2. Trials were repeated if the saccade latency was shorter than 80 ms or longer than 800 ms. Trials were excluded if saccades had starting positions more than 1° away from the central fixation cross or gross amplitude errors (<6.2° degrees or >25° degrees). These exclusion criteria led to loss of 20.5% of trials.

In the remaining valid trials, we calculated the directional error rate, mean saccade latency, and mean saccade accuracy for each block and each motivational condition for each subject. Directional errors were responses with a horizontal vector in the wrong direction (e.g. left instead of right). As expected, prosaccade directional errors were few, 0.1% (SD 0.6) in the noncontingent session and 0.3% (SD 1.0) in the contingent session: hence, only the antisaccade directional errors were analyzed. The latency and accuracy analyses were conducted only on directionally correct prosaccades and antisaccades. Accuracy of correct saccades was measured as the absolute distance between the saccade end point and the desired goal: hence, it reflected deviations in both direction and amplitude. These mean variables were subjected to repeated measures ANOVA using JMP 8.0.2 (http://www.jmp.com, SAS, Cary, North Carolina).

First, we assessed the noncontingent sessions. We used a general linear model ANOVA with main factors of saccade type (prosaccade, antisaccade), motivation (neutral, penalty, reward), and visual target/cue congruency (same, opposite), with subjects as a random factor. We did not enter the no-cue condition into this analysis because congruency is not a valid classification for these trials: rather, we used these data merely as a baseline in the figures.

Second, we assessed the effects of spatial contingency on saccades: that is, how saccades were affected when the consequence was contingent on the cue's location. First, we assessed this for the prosaccade data, using a repeated measures ANOVA with main factors of contingency (contingent, noncontingent), motivation (neutral, penalty, reward), and visual target/cue congruency (same, opposite), with subjects as a random factor. A priori linear contrasts were also used to compare each of the six different trial types (three motivational conditions×two visual target/cue congruency) between the contingent and noncontingent sessions. This analysis included all 16 subjects. For the antisaccade data, separate repeated-measures ANOVAs (as for prosaccades) were conducted for participants for whom consequence occurred when the cue and stimulus appeared on the same side, and those for whom the cue and the required movement were on the same side.

[1] The first group consisted of 6 males and 2 females, two of whom were smokers, with a mean age of 22.0 years (range 21–25); the second group consisted of 4 males and 4 females, one of whom was a smoker, with a mean age of 21.6 years (range 18–27). There was no difference between the groups in age ($t(7)=0.34$, $P=0.74$).
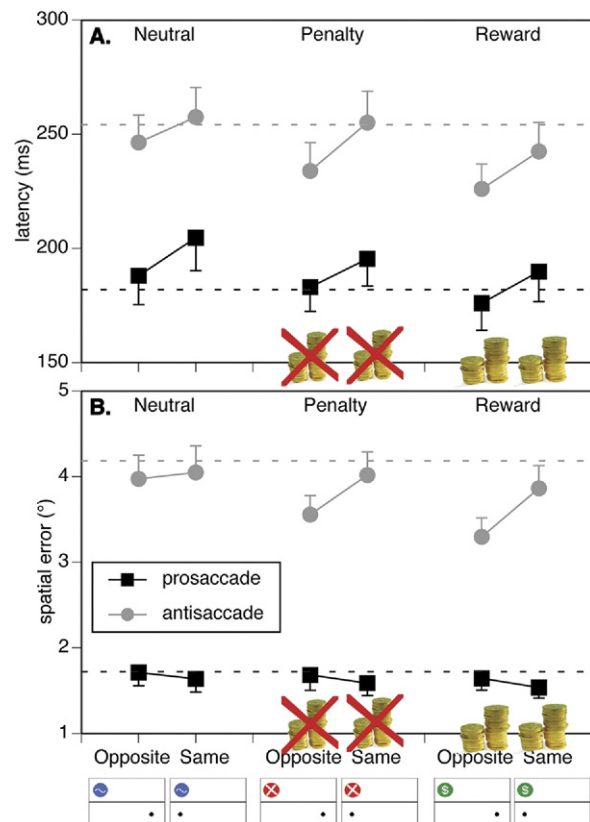

Fig. 2. Noncontingent results. (A) Mean latency and (B) mean spatial accuracy. In each graph, the same and opposite trials for visual target/cue congruency are shown for each of the three motivational conditions: neutral, penalty, and reward. Cartoons below illustrate the relation between cue and visual target for that condition: "same" refers to trials where the visual target (black dot) appeared in the same location as the motivational cue (coloured discs), and "opposite" for trials where they were on different sides. Coin stacks indicate the trial types in which rewards or penalties applied—in this noncontingent case, regardless of visual target/cue congruency. Horizontal dotted lines indicate the baseline for the no-cue condition, black for prosaccades, gray for antisaccades. Error bars indicate one standard error. For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.

RESULTS

Noncontingent sessions

For latency (Fig. 2A), prosaccades were faster than antisaccades ($F(1,165)=38.8$, $P<.0001$). There was also a main effect of motivation ($F(2,165)=11.9$, $P<.0001$): penalty trials were faster than neutral trials ($F(1,165)=4.08$, $P<.045$), and reward trials were faster than both neutral ($F(1,165)=23.6$, $P<.0001$) and penalty trials ($F(1,165)=8.07$, $P<.005$). There was a main effect of visual target/cue congruency ($F(1,165)=23.8$, $P<.0001$), with responses faster when visual targets appeared on the side opposite to the cue. No interactions were significant.

For spatial accuracy of correct responses (Fig. 2B), prosaccades were more accurate than antisaccades ($F(1,165)=812$, $P<.0001$). There was also a main effect of motivation ($F(2,165)=3.86$, $P<.025$): linear contrasts showed only that reward trials were more accurate than

neutral trials ($F(1,165)=7.74$, $P<.007$). There was a trend to a main effect of visual target/cue congruency ($F(1,165)=3.31$, $P<.07$), and the interaction between saccade type and visual target/cue congruency was significant ($F(1,165)=9.22$, $P<.003$). Although prosaccade accuracy did not differ by visual target/cue congruency, antisaccades were more accurate when stimuli appeared opposite to the side of the cue ($F(1,165)=11.8$, $P<.0008$), contrary to a speed-accuracy trade-off.

Although the three-way interactions were not significant for either latency or spatial accuracy, inspection of Fig. 2 suggests that the effect of visual target/cue congruency on antisaccades may have been greater for the penalty and reward conditions than for the neutral condition, suggesting a weak directional effect of motivation. For antisaccade latency, post-hoc linear contrasts showed an effect of visual target/cue congruency in penalty ($F(1,165)=7.31$, $P<.008$) and reward conditions ($F(1,165)=4.97$, $P<.028$), with a trend in the neutral condition ($F(1,165)=2.96$, $P=.09$). For antisaccade spatial accuracy, post hoc linear contrasts showed an effect of visual target/cue congruency in penalty ($F(1,165)=6.19$, $P<.014$) and reward conditions ($F(1,165)=9.33$, $P<.003$), with no effect in the neutral condition ($F(1,165)=0.16$, $P=.69$).

To summarize, the most prominent effect of motivation was to make responses faster and more accurate in general, more so with reward than with penalty, for both antisaccades and prosaccades. Regarding visual target/cue congruency, both prosaccade and antisaccade responses were faster—and antisaccades also more spatially accurate—when the visual target occurred at the location opposite to the cue, in all motivational conditions, consistent with a stimulus-based inhibition-of-return effect for both prosaccades and antisaccades. We did not find that this inhibition-of-return effect was reversed or minimized by reward in prosaccades, as reported in monkeys (Peck et al., 2009). Rather, post hoc analyses suggested that, if anything, this inhibition-of-return effect may have been accentuated by reward or penalty in the case of antisaccades.

Effects of contingency on prosaccades

For latency (Fig. 3A), there was a main effect of contingency ($F(1,165)=7.03$, $P<.009$) with prosaccades from contingent sessions slightly slower than in noncontingent sessions, when financial consequences did not depend on the relationship between visual target and cue location. There was a main effect of visual target/cue congruency ($F(1,165)=14.5$, $P<.0002$): again, responses were faster when stimuli were on the side opposite to the cue. There was a trend to an effect for motivation ($F(2,165)=2.58$, $P=.07$) and to an interaction between contingency and motivation ($F(2,165)=2.33$, $P=.09$). Linear contrasts showed that although contingency did not affect neutral or penalty trials, it increased latencies in reward trials ($F(1,165)=10.03$, $P<.002$). A priori linear contrasts showed that contingency increased latency for trials in the reward condition when stimuli appeared opposite to the cue
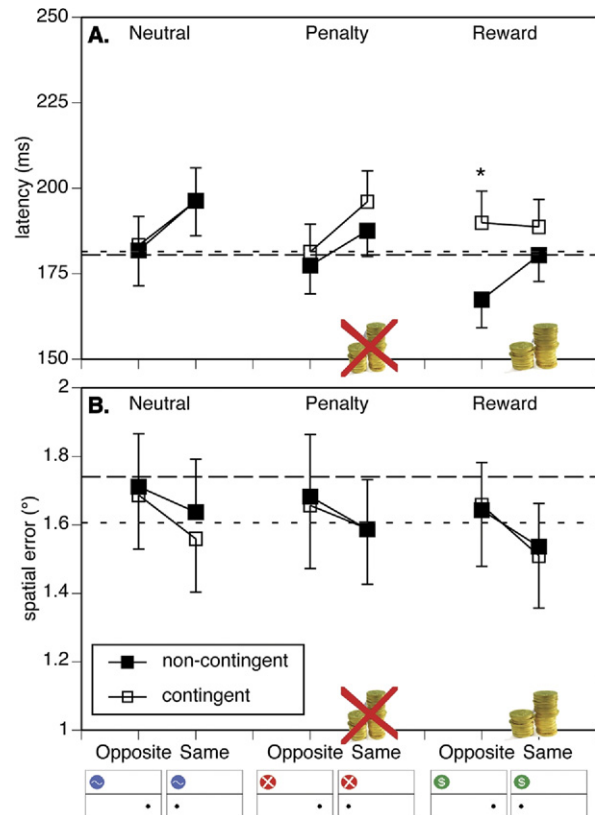

Fig. 3. Effects of contingency on prosaccades. (A) Mean latency and (B) mean spatial accuracy. In each graph, the same and opposite trials for visual target/cue congruency are shown for each of the three motivational conditions: neutral, penalty, and reward. Cartoons below illustrate the relation between cue and visual target for that condition: "same" refers to trials where the visual target (black dot) appeared in the same location as the motivational cue (coloured disc), and "opposite" for trials where they were on different sides. Horizontal lines indicate the baseline for the no-cue condition, dotted for the noncontingent session, and dashed for the contingent session. Coin stacks and arrows indicate the trial type where rewards or penalties applied in the contingent sessions, which were the trials in which the visual target and the cue were congruent. In the noncontingent session, as in Fig. 2, rewards and penalties applied for both same and opposite trial types. The asterisk indicates where a priori linear contrasts showed a significant difference between noncontingent and contingent sessions. Error bars indicate one standard error. For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.

($F(1,165)=10.7$, $P<.002$), that is, in the direction that was not rewarded.

For saccadic accuracy (Fig. 3B), there was no main effect of contingency or motivation, or any interaction involving these variables. There was a main effect of visual target/cue congruency ($F(1,165)=4.4$, $P<.04$), with responses slightly less accurate when stimuli appeared opposite to the side of the cue: together with the latency data, this would suggest a small speed-accuracy trade-off for the effect of visual target/cue congruency on prosaccades in general. A priori linear contrasts confirmed a lack of effect of contingency for any trial type.

To summarize, contingency had little effect on saccadic accuracy, but for latency, in the reward condition, the

benefit generated by reward in the noncontingent session was retained at the rewarded location but lost at the unrewarded location. This indicates a focusing of performance enhancement on the rewarded spatial location, which had the effect of negating the inhibition-of-return effect.

Effects of contingency on antisaccades

Group 1. In these subjects, contingency limited financial consequences to trials with the visual target on the same side as the cue. For latency (Fig. 4A), there was a main effect of motivation ($F(2,77)=5.17$, $P<.008$): neutral trials had slower responses than penalty ($F(1,77)=5.28$, $P<.03$) or reward trials ($F(1,77)=9.60$, $P<.003$), but reward and penalty trials did not differ from each other. There was a trend to an interaction between contingency and visual target/cue congruency ($F(1,77)=3.42$, $P<.07$): contingency in-

creased latency when the stimulus was on the side opposite to the cue ($F(1,77)=5.64$, $P<.02$), but not when the stimulus was on the same side, which was the response with financial consequences. *A priori* contrasts confirmed trends for contingency to increase latency when the stimulus was opposite to the cue for the penalty ($F(1,77)=3.06$, $P<.08$) and reward trials ($F(1,77)=3.05$, $P<.08$).

For spatial accuracy (Fig. 4B), there was only a main effect of contingency ($F(1,77)=6.69$, $P<.012$), with antisaccades more accurate in the contingent sessions. No *a priori* contrasts were significant.

For directional errors (Table 1), there was a main effect of contingency ($F(1,77)=8.78$, $P<.004$), with fewer errors in the noncontingent session. There was a main effect of motivation ($F(1,77)=10.16$, $P<.0001$): neutral trials had more errors than penalty ($F(1,77)=9.99$, $P<.003$) or re-
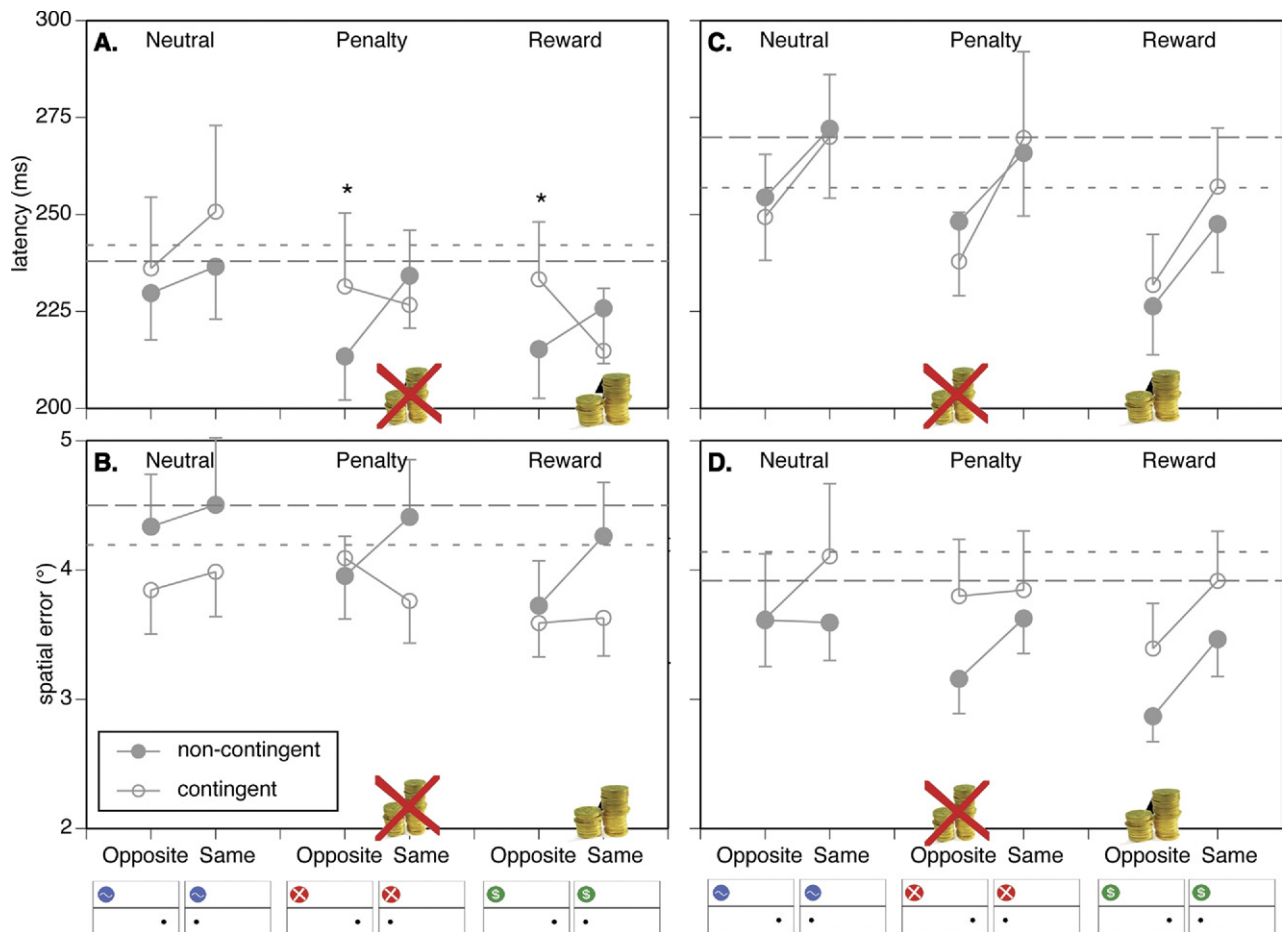

Fig. 4. Effects of contingency on antisaccades. Top graphs (A, C) show mean latency, bottom graphs (B, D) show mean spatial accuracy. Graphs A and B on the left are data from subjects who performed the contingent sessions in which financial consequences occurred for trials with the visual target on the same side as the cue, as indicated by the coin stacks, whereas graphs C and D on the right are from subjects in whom contingent sessions had financial consequences for trials with the visual target on the side opposite to the cue, again as indicated by the coin stacks. In the noncontingent session, as in Fig. 2, rewards and penalties applied for both trial types of those conditions. In each graph, the opposite and same trials for visual target/cue congruency are shown for each of the three motivational conditions: neutral, penalty, and reward. Cartoons below illustrate this relation between cue and visual target for that condition: "same" refers to trials where the visual target appeared in the same location as the motivational cue, and "opposite" for trials where they were on different sides. Horizontal lines indicate the baseline for the no-cue condition, dotted for the noncontingent session, and dashed for the contingent session. Asterisks indicate where *a priori* linear contrasts showed a significant difference between noncontingent and contingent sessions. Error bars indicate one standard error. For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.

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Table 1. Antisaccade directional error rate

	Noncontingent block		Contingent block	
	Mean	s.e.	Mean	s.e.
Group 1				
Neutral				
Opposite	4.38	1.54	6.70	1.72
Same	4.56	2.41	7.24	4.07
Penalty				
Opposite	2.08*	1.02	3.95	1.11
Same	1.99*	1.05	5.18*	1.73
Reward				
Opposite	1.74*	1.01	4.34	2.10
Same	0.69*	0.44	1.77*	0.69
Group 2				
Neutral				
Opposite	5.19	2.84	3.35	1.48
Same	4.82	1.87	4.48	1.95
Penalty				
Opposite	5.08*	2.70	1.79*	1.02
Same	4.67*	1.83	1.25	0.61
Reward				
Opposite	3.57*	1.35	2.04*	0.61
Same	1.77*	0.74	1.13	0.55

Asterisks indicate trials with financial consequences.

ward trials ($F(1,77)=19.0$, $P<.0001$), with penalty and reward trials similar to each other.

To summarize, we found again general beneficial effects of reward and penalty, with fewer directional errors and faster responses. As with prosaccades, making financial consequences contingent on the spatial location focused the latency benefits on those trials alone, so that trials in the unrewarded direction were no faster than those in the neutral condition, and the inhibition-of-return effect was again negated. In contrast to prosaccades, this was observed not only for reward trials but also for penalty trials.

Group 2. In these subjects, contingency limited financial consequences to trials with the stimulus on the side opposite to the cue. There was no main effect or interaction involving contingency in saccadic latency (Fig. 4C). As before, there was a main effect of motivation ($F(1,77)=5.63$, $P<.006$), with reward trials generating faster latencies than either penalty ($F(1,77)=5.33$, $P<.02$) or neutral trials ($F(1,77)=10.6$, $P<.002$). There was a main effect of visual target/cue congruency ($F(1,77)=18.6$, $P<.0001$), with responses faster when the visual target appeared on the side opposite to the cue.

Spatial accuracy data (Fig. 4D) showed a main effect of contingency ($F(1,77)=7.75$, $P<.007$), with antisaccades less accurate in the contingent session. However, none of the *a priori* contrasts were significant. There was a main effect of visual target/cue congruency ($F(1,77)=6.13$, $P<.016$), with responses more accurate when the visual target appeared opposite to the cue.

For antisaccade directional error rate (Table 1), there was a main effect of contingency ($F(1,77)=9.10$, $P<.004$),

with fewer errors in the contingent session. Again, there was a main effect of motivation ($F(1,77)=11.2$, $P<.0001$), with linear contrasts showing more errors on neutral trials than on penalty ($F(1,77)=12.38$, $P<.0008$) or reward trials ($F(1,77)=20.13$, $P<.0001$), but with no difference between penalty and reward trials.

To summarize, as with group 1, there were general beneficial effects of reward and/or penalty on directional errors and response time. However, contingency did not create directionally specific effects on latency in this group, with regard to visual target/cue congruency. This is understandable when we consider that in this contingent situation, any speeding of responses on trials with financial consequences would merely reinforce the underlying inhibition-of-return effect, rather than counteract it. Hence, both contingent and noncontingent sessions show faster responses when the stimulus appears opposite to the side of the cue.

DISCUSSION

We investigated how reward cues interact with spatial attention by examining human saccade latency and accuracy to locations previously occupied by cues. We found a general benefit of motivation (either reward or penalty) on latency and accuracy of all saccades. This replicates prior findings for reward (Watanabe et al., 2001; Roesch and Olson, 2004; Bendiksby and Platt, 2006; Kobayashi et al., 2006; Peck et al., 2009), as well as a number of human studies that examined reward and penalty conditions for antisaccades (Jazbec et al., 2005, 2006; Hardin et al., 2007; Mueller et al., 2010). However, unlike a recent study using monkeys (Peck et al., 2009), we did not find that the motivational value of cues modulated prosaccades contingent on cue location. The overriding effect was an inhibition-of-return effect at the cue location regardless of its valence. With regard to our three additional questions, first, with regard to motivational valence, the effects of penalty were in the similar direction as reward but generally intermediate in magnitude. Second, although antisaccades require greater attentional processing than prosaccades, we found that reward and penalty affected both responses similarly, apart from some modest post-hoc evidence that motivational cues might enhance the inhibition-of-return effect in antisaccades alone. Third, when reward was made contingent on the relationship between cue location and visual target location, similar efficiency gains were found for actions that would be rewarded, whereas actions that were now unrewarded lost the gains they had obtained from reward in the noncontingent trials.

The spatial effects of motivational cues on performance

Underlying most of our trials was an inhibition-of-return effect that made responses slower and less accurate when the visual target appeared at the same location as the cue. Inhibition-of-return is the phenomenon of slower return of attention to recently inspected locations relative to new locations (Posner et al., 1985), which is posited to be

beneficial in maximizing efficiency of visual search by preventing attention from returning to already examined locations (Klein, 1988; Dodd et al., 2009; Wang and Klein, 2010). In noncontingent trials, where reward or penalty did not depend on the location of the visual target in relation to the cue, we found only slight evidence that motivation modulated this inhibition-of-return pattern. The monkey prosaccade data (Peck et al., 2009) had shown a similar inhibition-of-return effect when cues indicated no reward; however, when cues indicated the presence of a reward, there was no effect of visual target/cue congruency for latency and, in fact, a reversal of the inhibition-of-return effect for accuracy. In contrast, for human prosaccades, we found no difference in the effects of visual target/cue congruency between neutral, reward, or penalty conditions. Hence, all three showed similar inhibition-of-return effects. For antisaccades, a post-hoc analysis suggested that, if anything, the inhibition-of-return effect may have been stronger with cues indicating reward or penalty, rather than minimized or reversed. Hence, the motivational valence of a cue has more modest visuospatial effects in humans, and does not confer benefits in visual attention at the location of the cue.

The effects of penalty versus reward

We found that the threat of a penalty created more variable effects than reward, being sometimes equivalent to reward trials (e.g. antisaccade directional error), sometimes equivalent to neutral trials (e.g. spatial accuracy in noncontingent trials), and sometimes intermediate between reward and neutral trials (e.g. latency in noncontingent trials). However, whenever an effect was present, it was always in the same direction as that of reward. Hence, saccadic performance does not follow the sign of motivational value (gain versus loss) but rather its unsigned value (the possibility of either gain or loss). In some respects, this may be considered consistent with a "mean variance" approach, in which responses track the probability of a financial consequence rather than its expected value (D'Acremont and Bossaerts, 2008). Neural responses approximating mean variance have been described in lateral orbitofrontal cortex (Tobler et al., 2007). This may appear to differ from the conclusion of Peck et al. (2009), who reported a "valence effect" in that reward cues attracted attention and neutral cues repelled attention. However, they did not include a penalty condition but simply conditions of reward or lack of reward. When we included penalties, which have a true "negative" value, we did not find attractive effects for reward and repulsive effects for penalty, as a valence account might predict. Rather, both enhance performance, with reward having a greater effect.

One can speculate on the reasons for a difference in the magnitude of response between penalty and reward. If the effects of both reward and penalty operate through attentional circuits, reward may simply receive more attentional priority than penalty. In contrast, differences may arise if reward and penalty are mediated in part by different processes. Matsumoto and Hikosaka (2007) have shown that the lateral habenula may be involved in penalty,

whereas dopaminergic neurons dominate with rewards. Prospect theory analyses have shown that gains and losses are perceived differently, for example, in the "endowment effect" (Thaler, 1980). Models of "subjective" or perceived value functions use different exponential terms for reward and loss (Kahneman and Tversky, 1979), and human functional imaging suggests a neural correlate in the inferior frontal gyrus (Votinov et al., 2010). These are mainly quantitative differences between reward and penalty, though, perhaps consistent with the fact that the effects of penalty in our study were similar but less in magnitude than those of reward. Regardless, the practical implication is that reward is a more efficient means of optimizing behavior than penalty.

The differential effects of motivation on prosaccades versus antisaccades

Antisaccades require subjects to look in the direction opposite to the visual target, a novel response for most humans (Hallett and Adams, 1980). We found the usual antisaccade effects: directional errors, shorter latencies, and greater spatial inaccuracy than for prosaccades (Munoz and Everling, 2004), consistent with greater demands on attention and cognitive control. Functional neuroimaging has shown increased activity in parietal and frontal eye fields during antisaccades, as well as in dorsolateral prefrontal cortex, anterior cingulate cortex, and supplementary eye fields (O'Driscoll et al., 1995; Sweeney et al., 1996; Connolly et al., 2002; Ford et al., 2005; Manoach et al., 2007b; Moon et al., 2007), and there are antisaccade-related anomalies in anterior cingulate cortex in autism spectrum disorders and schizophrenia (Manoach et al., 2007a; Thakkar et al., 2008; Agam et al., 2010). These findings are of interest because recent studies of reward have shown that, along with orbitofrontal cortex, anterior cingulate cortex forms an important part of the dopaminergic cortical-basal ganglia circuit involved in reward processing (Doya, 2008; Haber and Knutson, 2010; Hewig et al., 2011; Hickey et al., 2010; Sescousse et al., 2010; Wallis and Kennerley, 2010). Whether the cingulate regions involved in reward-based attention and those in the attentional control required by antisaccade generation overlap is not yet known.

Our results first showed similar general effects of reward more than penalty in reducing latencies, for both prosaccades and antisaccades. Prior human studies have produced mixed results: some failed to find incentive effects on latency of either type of saccade (Duka and Lupp, 1997; Jazbec et al., 2006; Mueller et al., 2010), whereas others have reported similar reward- and penalty-induced reductions in antisaccade latencies, but did not examine prosaccades (Jazbec et al., 2005; Hardin et al., 2007). Studies that used blocks of randomly mixed prosaccades and antisaccades (Jazbec et al., 2006; Mueller et al., 2010) may have had more difficulty in discerning reward-based latency effects because of mixing and switching costs (Manoach et al., 2002). Nevertheless, even these studies found that reward improved the directional accuracy of antisaccades (Duka and Lupp, 1997; Jazbec et al., 2006;

Mueller et al., 2010), with either minimal or no effect on prosaccade accuracy.

In our study too, other effects of motivation were more evident in antisaccades than in prosaccades. Motivation enhanced inhibition-of-return effects in the spatial accuracy of antisaccades but not of prosaccades. Enhancement for rewarded locations in the contingent condition could be seen for both penalty and reward in antisaccade latencies, but only for reward in prosaccades. In part, greater improvement for antisaccades than prosaccades could reflect the fact that, as nearly automatic responses, prosaccades may already be near optimal performance. Alternatively, the greater attentional control involved in antisaccades may render them more sensitive to reward modulation.

The influence of spatial contingency on the effects of motivation

The main effect of making reward contingent on stimulus location was to confine gains to the rewarded locations. Contingency did not make rewarded locations faster and leave unrewarded locations unchanged compared with noncontingent trials. Rather, rewarded locations remained similar but unrewarded locations reverted back to the performance in the neutral (no-reward) condition. This was mainly evident when the attentional enhancement of reward or penalty opposed the direction of the inhibition-of-return effect. These results suggest first, that the reward system has sufficient capacity to enhance performance at multiple sites at a near optimal level. Second, contingency allows subjects to efficiently focus attention on and limit benefits to the rewarded response. This latter result is compatible with neural coding of action value in area LIP (Platt and Glimcher, 1999; Dorris and Glimcher, 2004; Sugrue et al., 2004).

CONCLUSION: VISUAL SELECTION VERSUS ACTION VALUE

The prior study in monkeys found that LIP neurons encoded the valence of reward cues in their receptive field, correlating with faster and more accurate prosaccades to visual targets at the cue location (Peck et al., 2009). The implication is that LIP provides a spatial map in which reward enhances visual rather than saccade selection (Gottlieb and Balan, 2010). This contrasts with proposals that LIP encodes action value (Platt and Glimcher, 1999; Dorris and Glimcher, 2004; Sugrue et al., 2004), in which neural activity is enhanced only for specific motor responses with reward value. Hence, action value cannot explain selective enhancement of performance for responses to targets at the former site of the cue, if reward is given regardless of target location.

We did not find selectively enhanced benefits at the cue location in noncontingent blocks. For antisaccades, we found the reverse of the monkey data: rather than facilitation, there was some evidence that reward or penalty increased inhibition at the location of the motivational cue. Nevertheless, this might still constitute evidence for mod-

ulation of visual selection for attentionally demanding saccades. At this point, it is unclear whether this would occur in LIP or in other attentional regions, such as the frontal eye field, orbitofrontal, dorsolateral prefrontal, or anterior cingulate cortex (Sumner, 2006; Manoach et al., 2007b; Schonberg et al., 2011). Finally, the fact that our contingent blocks showed that benefits became selective for the rewarded response is consistent with the action value hypothesis (Platt and Glimcher, 1999; Dorris and Glimcher, 2004; Sugrue et al., 2004). Our findings thus illustrate some important differences and similarities between humans and monkeys in the impact of reward on saccades, with relatively modest effects on visual selection if any, and stronger effects on motor selection.

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