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Abstract

The aim of this study was to examine the neural bases for perceptual-cognitive superiority in a soccer anticipation task using functional magnetic resonance imaging (fMRI). Thirty-nine participants lay in an MRI scanner while performing a video-based task in which they predicted an oncoming opponent's movements. Video clips were occluded at four time points; and participants were grouped according to in-task performance. Early occlusion reduced prediction accuracy significantly for all participants, as did the opponent's execution of a deceptive maneuver; however, high-skill participants were significantly more accurate than their low-skill counterparts under deceptive conditions. This perceptual-cognitive superiority was associated with greater activation of cortical and subcortical structures involved in executive function and oculomotor control. The contributions of the present findings to an existing neural model of anticipation in sport are highlighted.

Keywords: Cognitive; Expert; Oculomotor; Perceptual; Sport.

1 (Kunde, Skirde, & Weigelt, 2011) – but experts may still require directional information such as
2 ball flight in order to move substantially beyond chance performance (Rowe, Horswill, Kronvall-
3 Parkinson, Poulter, & McKenna, 2009).

4 Although the accumulation of perceptual experience underpins many explanations for
5 anticipation skill superiority, others have suggested that because action perception and execution
6 share common neural origins (Prinz, 1997), then it is motor expertise, be it in deception or
7 otherwise, that determines the extent of this advantage. This notion is corroborated by
8 investigations of the mirror neuron system (MNS), a parieto-frontal network of neurons that are
9 similarly active when individuals perform, imagine or witness an action within their own
10 repertoire (Rizzolatti & Maddalena Fabbri, 2007). Subtle differences in this MNS motor
11 resonance when viewing and predicting sporting actions are manifest in behavioral (Knoblich &
12 Flach, 2001) neuroimaging (Calvo-Merino, Grèzes, Glaser, Passingham, & Haggard, 2006) and
13 psychophysiological (Aglioti, Cesari, Romani, & Urgesi, 2008) data.

14 The roles of neural systems in sport anticipation have been investigated more extensively
15 in recent years. Wright and Jackson (2007) employed the temporal occlusion paradigm to
16 examine novice tennis players' cortical fMRI activation when predicting an opponent's serve
17 direction. Action prediction significantly activated MNS regions when contrasted with a passive
18 observation condition. Wright, Bishop, Jackson, and Abernethy (2010) subsequently found
19 stronger activations for early- than for late-occluded sequences of a badminton shot, notably in
20 premotor MNS regions and in medial frontal cortex (MFC). Experts also exhibited greater frontal
21 MNS and MFC activation than did novices when viewing the early-occluded sequences. To
22 assess the relative contribution of kinematic information to these differences, Wright, Bishop,
23 Jackson and Abernethy (2011) compared expert, intermediate and novice badminton players'

1 responses to normal video and point-light displays of opponents in a badminton prediction task.
2 Activations were highly similar for both video formats, reinforcing the prominence of kinematic
3 information; moreover, greater frontal activity was apparent in experts when viewing early-
4 occlusion sequences. There was also evidence for suppression of low-level, task-irrelevant
5 stimuli in experts, suggesting greater attentional efficiency. However, experts' comparatively
6 high levels of activation in anticipation tasks stands in sharp contrast to that witnessed during
7 imagery of a self-paced sport: Milton, Solodkin, Hlušík, and Small (2007) compared the neural
8 activity of expert and novice golfers as they mentally prepared for a hypothetical putt shot. The
9 authors found almost ubiquitously stronger activation in novices, in areas of the brain associated
10 with motor planning and execution – most notably the basal ganglia; this collection of nuclei are
11 pivotally involved in decision making and subsequent action selection, making reciprocal
12 connections with motor and premotor areas of the cortex. Milton et al. interpreted the
13 comparatively lower activity in experts as a reduction in the complexity of dynamic motor
14 control, thereby promoting greater movement consistency.

15 Milton et al.'s (2007) findings contrast with the very active role for the basal ganglia
16 proposed by Yarrow, Brown and Krakauer (2009) in their *affordance competition model* of
17 motor preparation and decision-making, based on Cisek's (2007) affordance competition
18 hypothesis. Yarrow et al. propose a complex cortico-subcortical network comprising not only
19 regions of the MNS, but also prefrontal cortex, ventral and dorsal visual pathways, and two
20 subcortical structures – the basal ganglia and the cerebellum. In this model, visual inputs are
21 transformed into motor plans, which may be manifested in commonly observed MNS resonance,
22 before the basal ganglia *behaviorally bias* the best possible motor action, by encoding the
23 difference between expected and actual reward of a given course of action (Stocco, Lebiere, &

1 Anderson, 2010) – ultimately leading to action execution; the hours of deliberate practice
2 accrued by expert performers (Ericsson, Krampe, & Tesch-Römer, 1993) may potentiate this
3 function of the basal ganglia. According to the model, the cerebellum is primarily involved in
4 transforming visual input into motor plans. However, activation in the culmen, a region of the
5 cerebellum, has been correlated with low response time variability in children performing a go-
6 nogo task (Simmonds, et al., 2007), which indicates a potential role for this region also in biasing
7 the correct response. Yarrow et al. propose that the basal ganglia and cerebellum serve important
8 functions in generating and selecting motor plans. Accordingly, we might expect greater
9 activation in superior anticipators, in both of these subcortical structures, which is contrary to
10 neural activity witnessed in golf putting (Milton, et al.) and in previous fMRI studies of
11 anticipation skill in sport (Wright, et al., 2010; Wright, et al., 2011).

12 The primary aim of this study was to provide an insight into those neural mechanisms
13 identified in the affordance competition model (Yarrow, et al., 2009) that may differentiate those
14 demonstrating superior anticipation skill from their lesser skilled counterparts, using rapidly-
15 occurring and unpredictable stimuli (see Mann, Williams, Ward, & Janelle, 2007); this is a novel
16 step for an fMRI study in sport. A second aim was to uncover a neural basis for the previously
17 identified expert advantage when confronted with deceptive actions, as this has hitherto received
18 no attention in neuroimaging studies of sport anticipation thus far. In accordance with existing
19 sport anticipation fMRI data (Wright, et al., 2010; Wright, et al., 2011) and research into
20 deception in sport (e.g., Jackson, et al., 2006; Kunde, et al., 2011), we propose four primary
21 hypotheses: (1) That high-skilled anticipators' superiority will be greatest when viewing early-
22 occluded sequences and when viewing deceptive footage; (2) that this group disparity will be
23 greatest when participants view deceptive footage at the earliest point of occlusion; (3) that there

1 will be comparatively higher levels of MNS and MFC activation in high-skilled anticipators
2 when predicting an oncoming opponent's actions; and (4) that the differences in MNS activation
3 will be greater still under combined early occlusion and deceptive conditions. Yarrow et al.'s
4 (2009) affordance competition model provides us with a useful basis for predictions, grounded as
5 it is in an extensive corpus of experimental and behavioral research; hence, we also cautiously
6 predict increased activation in superior anticipators, of basal ganglia and cerebellar nuclei.

7 **Methods**

8 **Participants**

9 A convenience sample of 41¹ male participants was recruited on the basis of their
10 competitive experience in soccer: Experiences ranged from none to regular semi-professional
11 competition. The study was approved by the Brunel University Research Ethics Committee in
12 accordance with the Declaration of Helsinki, and all participants gave their informed consent
13 prior to participation. Two participants' data were excluded from the analysis, due to a z-plane
14 drift in excess of 2 millimeters from their original position during fMRI data acquisition. Soccer
15 playing expertise is a concatenation of many attributes, one of which is anticipation skill (Reilly,
16 et al., 2000). Therefore, in order to specifically examine the neural mechanisms underpinning
17 anticipation skill in the present task, overall prediction accuracy was used to categorize
18 participants; this criterion has recently been advocated as a valid means by which differences in
19 sport anticipation skill may be investigated (Huys, et al., 2009; Roca, Williams, & Ford, 2012;
20 Vaeyens, Lenoir, Williams, & Philippaerts, 2007; Williams & Ericsson, 2005; Williams & Ford,
21 2008). Consequently, the remaining 39 participants ($M_{\text{age}} = 22.5$ yrs, $SD = 3.73$ yrs) were
22 classified post hoc into three groups differing in anticipation skill: Low-skill anticipators (chance
23 level performance or below, $n = 11$; mean competitive experience [M_{exp}] = 2.4 yrs, $SD = 4.1$ yrs),

1 intermediate-skill anticipators (51-59% accuracy; $n = 14$; $M_{\text{exp}} = 10.2$ yrs, $SD = 6.0$ yrs) and
2 high-skill anticipators ($\geq 60\%$ accuracy, $n = 14$, $M_{\text{exp}} = 13.2$ yrs, $SD = 3.1$ yrs).

3 **Stimuli**

4 We filmed sequences of three junior international level soccer players dribbling towards a
5 video camera (NV GS400; Panasonic Corporation, Secaucus, NJ) placed at a distance of 11.5
6 meters from the start of the players' run, in an indoor sports hall. The actors ran toward the
7 camera and then moved obliquely in a predetermined direction (left/right), as they would when
8 attempting to evade a defending player's interception. They performed a deceptive maneuver
9 known as a *stepover* in 50% of runs immediately prior to direction change; for the remaining
10 50% of prediction trials no deception was performed. Video clips were edited using video editing
11 software (Pinnacle Studio Pro v. 11.0, Pinnacle Systems, Mountain View, CA) to create four
12 levels of temporal occlusion for each video format: At the point of direction change (t_0), 160 ms
13 prior to t_0 (hereafter -160 ms), 80 ms prior to t_0 (-80 ms), and 80 ms after t_0 (+80 ms). Forty-
14 eight experimental video clips (3 actors x 2 directions x 2 levels of deception x 4 iterations) and
15 24 control clips of the same soccer players walking casually across the field of view with the ball
16 were created and presented on six occasions each, yielding a total of 432 stimuli. No anticipation
17 was required in the control clips, which enabled a contrast with experimental clips, for levels of
18 MNS activation.

19 **fMRI Data Acquisition**

20 We acquired functional and structural images on a Trio 3T MRI scanner (Siemens,
21 Erlangen, Germany) via an eight-channel array head coil. For each functional run, a standard,
22 whole brain, echo planar gradient-echo imaging sequence was used to acquire 41 transverse

1 slices (3 mm thickness, TR 3000 ms, TE 31 ms, flip angle = 90°). Whole brain anatomical data
2 were collected using a 176 slice, 1 mm³ voxel size, MP-RAGE T1-weighted sequence.

3 **Experimental Procedure**

4 Participants were familiarized with both the experimental protocol and the scanner
5 environment prior to commencing the study. Each participant lay in the supine position in the
6 scanner while viewing back-projected video stimuli via an overhead mirror. For experimental
7 stimuli, they were required to press one of two buttons on an MRI-compatible response box
8 (LUMItouch™; Photon Control, Inc., Burnaby, B.C., Canada) to indicate the direction in which
9 they believed the video clip actor would move (left/right); they pushed a third button to indicate
10 control footage. Participants were asked to respond as quickly and accurately as possible.
11 Prediction accuracy and response time were collected via experiment generator software (E-
12 Prime v.2.0, Psychology Software Tools, Inc., Pittsburgh, PA). Stimuli were blocked according
13 to level of occlusion; the order in which blocks were viewed was partially counterbalanced
14 across all participants. Presentation of the three video clip types (deceptive/non-
15 deceptive/control) was automatically randomized within each block. A total of 108 clips, each
16 lasting approximately 2 s, were presented in each of the four occlusion blocks. All clips were
17 followed by a blank gray screen lasting 1.7 s, during which participants registered their response.
18 Participants performed a simple visual cognition task for one minute between blocks. Thus, each
19 block lasted approximately 400 s. On-screen instructions gave additional guidance to the
20 participants. Brain imaging data were acquired throughout.

21 **Data Analysis**

22 **Response data.** Response data were analyzed not only to confirm the validity of the
23 within-task criterion for group formation, but also to investigate the extent to which performance

1 was mediated by factors such as level of occlusion and deception; hence, a mixed Group (high-,
2 intermediate-, and low-skill) x Occlusion (-160 ms, -80 ms, t0, +80 ms) x Condition (control,
3 deception, no deception) factorial MANOVA was applied to the data. Due to a button box fault,
4 one high-skill participant did not contribute response data. All analyses were performed using
5 PASW Statistics 18 (v 18.0; IBM, Armonk, NY). Where significant main effects or interactions
6 were detected, simple main effects analysis followed using one-way ANOVA and Tukey's post
7 hoc test, or dependent t-tests where appropriate. Significance was accepted at $p < .05$.

8 **fMRI data.** Brain imaging data were analyzed using SPM8
9 (<http://www.fil.ion.ac.uk/spm>). Functional images were spatially realigned to the first image in
10 the series then co-registered with the T1 image. Images were normalized to the Montreal
11 Neurological Institute (MNI) template then smoothed using a Gaussian kernel of 7 mm full-
12 width half-maximum. The design matrix convolved the experimental design with a
13 haemodynamic response function. The model was estimated using proportional scaling over the
14 session to remove global effects, and with a high pass filter of 128 s. Contrasts were computed to
15 assess the change from the implicit baseline in each combination of experimental conditions, for
16 each participant. Random effects analysis was performed by entering the contrast images derived
17 into SPM's full factorial model. For each experimental contrast, significantly activated voxels
18 were to be defined as those within the whole-brain smoothed grey matter mask that satisfied a
19 familywise error (FWE) rate of $p < .05$ and exceeded an extent threshold of 20 voxels. We
20 labeled brain locations of the peaks of activation with reference to anatomical landmarks and
21 Brodmann areas (BAs) using WFU PickAtlas (Maldjian, Laurienti, Kraft, & Burdette, 2003).

Results

Response Data

Analyses revealed significant main effects of Group, Wilks' Lambda (.27), $F(4,68) = 15.93$, $\eta_p^2 = .48$, $p < .001$; Occlusion, Wilks' Lambda (.08), $F(6,30) = 56.10$, $\eta_p^2 = .92$, $p < .001$; and Condition, Wilks' Lambda (.02), $F(4,32) = 324.57$, $\eta_p^2 = .98$, $p < .001$. Univariate tests, pairwise comparisons and descriptive statistics for all main effects are shown in Table 1².

There were significant interactions for Group x Condition, Wilks' Lambda (.39), $F(8,64) = 4.90$, $\eta_p^2 = .38$, $p < .001$ and Occlusion x Condition, Wilks' Lambda (.09), $F(12,24) = 19.25$, $\eta_p^2 = .91$, $p < .001$. Follow-up univariate tests revealed that differences in Prediction Accuracy accounted for the observed Group x Condition interaction, $F(4,315) = 20.84$, $\eta_p^2 = .54$, $p < .001$; however, paired t tests showed that all participants were significantly more accurate when viewing control footage than in the experimental conditions, and when viewing non-deceptive, as compared with deceptive, footage $p < .005$. Differences in both Prediction Accuracy, $F(6,210) = 59.47$, $\eta_p^2 = .63$, $p < .001$ and Response Time, $F(6,210) = 5.07$, $\eta_p^2 = .13$, $p < .001$ accounted for the Occlusion x Condition interaction: paired t tests showed that Prediction Accuracy was greater for the Control condition than for predictive conditions at the three earliest levels of Occlusion, $p < .001$, but not at $t + 80$ ms, $p > .05$. Additionally, participants took significantly longer to respond to deceptive footage than they did to non-deceptive footage at the two later levels of Occlusion, $p < .001$. Group x Occlusion and Group x Occlusion x Condition interactions did not reach significance, $p > .05$. The simple main effects of Group for prediction accuracy at each level of Condition and Occlusion are displayed in Figure 1.

1 **fMRI Data**

2 There were significant main effects of Group, Occlusion and Condition (FWE-corrected
3 $p < .05$). On closer scrutiny, some contrasts contributed more strongly than others to these
4 effects; these activations, which met the stringent threshold criteria, are shown in Table 2.³
5 Activation in cerebellum (pyramis, culmen), inferior visual cortex, superior temporal gyrus and
6 precuneus differentiated high-skill anticipators from their intermediate- and low-skill
7 counterparts when seeking to predict an opponent's movements. Further, when visual
8 information was most restricted (i.e., at the earliest level of occlusion), there was also activation
9 of a combination of cortical and subcortical structures – basal ganglia (lentiform nucleus in Table
10 2), thalamus, cingulate/supplementary eye field. Additionally, the greatest activation differences
11 in high-skill participants occurred between the two earliest levels of occlusion – 160 ms and 80
12 ms prior to the opponent's direction change; the foci were in superior temporal gyrus, superior
13 and inferior parietal lobules, and superior frontal gyrus. Figure 2 shows the loci of activations in
14 high-skill anticipators for each of three contrasts, in cerebellum (pyramis), basal ganglia
15 (lentiform nucleus), and anterior cingulate cortex (ACC).

16 The data from the Prediction > Control contrast did not show any significant foci at the
17 original display threshold criterion ($p < .05$, FWE-corrected for multiple comparisons), which
18 may be the result of a diminished contrast-to-noise ratio for these rapidly alternating stimuli.
19 However, at a lowered voxel-wise threshold of $p < .005$ (uncorrected), activation patterns were
20 similar to those found for both novices and experts in earlier studies of badminton (Wright, et al.,
21 2010; Wright, et al., 2011), in which prediction and control conditions were separately blocked.
22 Areas included precuneus, premotor cortex, extrastriate cortex, inferior frontal gyrus, superior
23 frontal gyrus, and supplementary eye fields (SEF). Loci of significant activations at the new

1 threshold, but at an extent threshold of 60 voxels, are shown for all participants combined in
2 Table 3. Figure 3 illustrates the activations witnessed for the same contrast (prediction vs.
3 control) for each of the three groups separately.

4 **Discussion**

5 The foremost contribution of this study was to identify potential neural bases for
6 anticipation skill superiority in soccer. Two additional novel developments on previous fMRI-
7 based studies of anticipation in sport (Wright et al., 2010; Wright et al., 2011) were (i) the
8 introduction of video clips in which the actor was performing a deceptive maneuver and (ii) the
9 randomized interspersing of these deceptive stimuli with non-deceptive and control clips so as to
10 reduce predictability – and therefore the potential for in-task learning. As per our first
11 hypothesis, the high-skill anticipators were significantly better than lesser skilled participants at
12 predicting opponents' actions in the deceptive condition – although this did not vary according to
13 level of occlusion, contrary to our second prediction. The understanding of others' actions was
14 reflected somewhat in brain activations, in line with our third hypothesis: There was evidence of
15 stronger activation of MNS (e.g., IPL, BA6) and related areas in high-skill participants when
16 compared to the intermediates, who in turn exhibited greater MNS activation than did the low-
17 skill group, when predicting an opponent's actions (see Figure 3; cf. Wright, et al., 2010; Wright,
18 et al., 2011) – albeit only when deceptive and non-deceptive conditions were examined
19 conjointly; there was also no apparent three-way interaction (i.e., differences in MNS activations
20 were not magnified when participants viewed early-occluded deceptive footage).

21 Also in keeping with our predictions, differences between the high-skilled and lower-
22 skilled participants were most clearly manifest in both behavioral and fMRI data when early-
23 occluded sequences were viewed, (i.e., when the least information was available), but the most

1 robust differences in neural activation – which included cortical and subcortical areas identified
2 in the affordance competition model – occurred consistently between high-skill and
3 intermediate/low-skill participants combined; there was negligible difference between the latter
4 two groups, which is noteworthy when considering that the intermediates had still accrued
5 considerably more competitive experience, on average, than their novice counterparts ($t[23] =$
6 $3.58, p < .005$). Thus, the brain activation differences witnessed may correspond to not only the
7 surpassing of a threshold for hours accumulated in practice/competition to become sufficiently
8 expert (see Ericsson, et al., 1993), but also the quality of such practice.

9 The strongest activation of MNS regions that correspond to those found in badminton
10 (Wright, et al., 2010; Wright, et al., 2011) were witnessed only in high-skill participants, when -
11 160 ms was contrasted with -80 ms (Table 2[d]). This is a somewhat unanticipated finding,
12 because we might expect greater MNS activation when an increased amount of familiar visual
13 information is presented, but this may simply reflect an increased level of engagement with the
14 more challenging brief stimulus duration. Indeed, this is consistent with the notion that early
15 occlusion actually increases participants' attention (Wright, et al., 2010). When novices' data
16 were considered in isolation (Figure 3), they did not exhibit significant MNS activation when
17 viewing the prediction sequences, relative to baseline, which is consistent with their comparative
18 lack of experiences in soccer and thus lack of familiarity with the actions performed, be they
19 deceptive or otherwise.

20 Similar to findings in tennis (Rowe, et al., 2009), but in contrast to findings from rugby
21 (Jackson, et al., 2006), the high-skill participants' performance in the presence of deception did
22 not move above chance level until t_0 – the point of direction change; however, intermediates'
23 performance did not do so until the opponent's final direction of movement was visible (+80

1 ms), and low-skill participants never rose above chance level. Thus, whilst the high-skill
2 participants were still being deceived regularly at the two earliest stages of occlusion, there was
3 clear behavioral (Figure 1) and neuroimaging evidence (Table 2) of their superiority. MNS
4 activation was not clearly apparent when the deceptive condition was considered in isolation,
5 contrary to our hypotheses. However, this may have been a function of a low signal-to-noise
6 ratio in the data, derived from rapid alternating presentation of video stimuli; this is a novel step
7 for such neuroimaging studies, but it is an important one if real world conditions faced are to be
8 approximated. Nonetheless, there was highly robust evidence ($p < .05$, FWE-corrected) for
9 activity in high-skill participants of a cortico-subcortical network of structures comprising
10 cerebellum, thalamus, basal ganglia and ACC; a network that has been implicated not only in
11 executive function (Heyder, Suchan, & Daum, 2004; Kim, Kroger, & Kim, 2011; Lütcke,
12 Gevensleben, Albrecht, & Frahm, 2009), but also oculomotor control (Heyder, et al., 2004;
13 Tanaka & Kunimatsu, 2011). Moreover, the cerebellar and basal ganglia activations are
14 consistent with the predictions of the affordance competition model (Yarrow, et al., 2009).

15 The single activation that discriminated high-skilled players from both intermediates and
16 low-skill participants when viewing deceptive maneuvers arose in a finite region of right ACC (x
17 $= 9$, $y = 17$, $z = 19$; cluster size = 22 voxels). We previously found right ACC activation in
18 badminton experts relative to novices, when they were required to respond to point-light
19 representations of opposing players' actions (Wright, et al., 2011); further fMRI data using point-
20 light displays will help us to better understand the informativeness of opponent kinematics, as
21 opposed to other cues (e.g., opponent's gaze), with regard to deception. The ACC has
22 consistently been identified as an important structure in the monitoring of response conflict,
23 specifically when a motor response is required (Turken & Swick, 1999) – and right-lateralized

1 activation reflects the processing of visuospatial stimuli (K. E. Stephan, et al., 2003). Highly
2 comparable activation has been shown in a similarly focalized and right-lateralized region of
3 ACC ($x = 5, y = 21, z = 34$) when participants either correctly rejected, or failed to reject,
4 incorrect stimuli in a *go-nogo* task (Lütcke & Frahm, 2008); similar activation was found in
5 rACC ($x = 9, y = 16, z = 32$) when participants were required to manage competing response
6 alternatives in a Stroop interference task (Kim, et al., 2011). Thus, the rACC activation
7 witnessed in the deceptive condition may represent not only the suppression of the high-skill
8 anticipators' prepotent responses to the deceptive maneuver – to anticipate/move in the direction
9 of the deception – but also to monitor any incorrect decisions made; this is comparable to the
10 role proposed for the basal ganglia in assessing the 'reward value' of potential response options
11 (Yarrow, et al., 2009).

12 Given the absence of any response accuracy differences at -160 ms, the latter rACC
13 function is the more likely of the two, for the present data. Such inhibition is highly adaptive in
14 situations for which the cost of not doing so may be high; for example, the tendency of handball
15 goalkeepers to perceive opponents' movements as deceptive may stem from a cost-benefits
16 analysis that ultimately favors caution (Cañal-Bruland & Schmidt, 2009). It is also noteworthy
17 that – peculiarly – all participants' performance in the Control condition was still not at 100%
18 accuracy, irrespective of level of occlusion, which suggests that key press errors occurred.
19 Performance for all participants in the non-deceptive condition was not only high, but also
20 largely equivalent, except at occlusion level t0-80 ms (see Figure 1), suggesting that the actors'
21 movement intentions were easy to predict in the absence of deception. Hence, the ability to
22 perceive, and then inhibit a prepotent response to, an opponent's deception could be a key factor
23 that discriminates perceptual-cognitively skilled soccer players from those not so skilled.

1 High-skill anticipators' activations at the earliest stage of occlusion comprised regions
2 similar to those previously identified as supplementary eye fields (SEF), regions of the frontal
3 lobes that are involved in the planning and control of saccadic eye movements (Amiez &
4 Petrides, 2009; Grosbras, Laird, & Paus, 2005; Pierrot-Deseilligny, Milea, & Müri, 2004) and of
5 a network comprising striatal (lentiform nucleus), thalamic and cingulate areas identified as co-
6 acting in executive control processes (Heyder, et al., 2004; Lütcke, et al., 2009). Not only do the
7 ventroanterior region of the thalamus and the basal ganglia appear to play important roles in the
8 generation of volitional saccades (Tanaka & Kunimatsu, 2011), but the latter also plays a key
9 role in biasing the correct motor response selection (Yarrow, et al., 2009). The greater cerebellar
10 activations in the high-skill anticipators are also consistent with the notion of increased
11 oculomotor activity and motor preparation (Simmonds, et al., 2007; Yarrow, et al., 2009); and
12 working memory-driven saccades (cf. Nitschke, et al., 2004; T. Stephan, et al., 2005). These
13 activations collectively suggest that skilled participants' performance incorporated better
14 preparation of intentional saccades, through biasing oculomotor activity, which relates well to
15 the commonly observed efficiency of expert visual search patterns (Gegenfurtner, Lehtinen, &
16 Säljö, 2011; Mann, et al., 2007).

17 Some of the activations observed are pertinent to the shifting of attention, rather than
18 saccadic activity, such as that observed in the lentiform nucleus (see Grosbras, et al., 2005). The
19 precuneus, an important part of the dorsal visual stream identified in the affordance competition
20 model (Yarrow, et al., 2009) that plays an integral role in orientation of attention (Cavanna &
21 Trimble, 2006) and execution of voluntary saccades (Grosbras, et al., 2005), was more active in
22 high-skilled participants as they viewed the shortest occlusion condition footage (-160 ms), when
23 contrasted with the next shortest (-80 ms), suggesting a change in attentional strategy when

1 confronted with very limited visual information. There is also evidence for superior shifting of
2 attention in high-skill anticipators across all levels of occlusion, in the activation of superior
3 parietal lobule. Almost identical activation has been found for exogenously controlled shifts of
4 attention (Molenberghs, Mesulam, Peeters, & Vandenberghe, 2007). If this is also the case for
5 our data, then high-skill participants' visual search/attentional strategy was predominantly
6 determined by features of the stimulus (e.g., the opponent's movements), not by a preconceived
7 plan as to which sections of the display would be most informative.

8 Given the complex, naturalistic qualities of the stimuli used in the present study, the
9 extent to which our data parallel those from the studies cited above, in which simple
10 experimental stimuli were used, is very encouraging. However, there was a notable absence of
11 co-activation of some structures, when we might reasonably have expected it, at the strict FWE
12 threshold; this may be a function of the experimental design. Further analyses from protocols
13 comprising longer blocks (~ 20 s) of deceptive stimuli may produce data that yield this co-
14 activation; however, the imperative to reduce predictability remains (see Mann, et al., 2007).
15 Functional connectivity analyses would confirm/disconfirm the proposed operations of the
16 affordance competition model (Yarrow, et al., 2009); the present data depict many robust
17 activations predicted by this model, but cannot tell us about interrelations between the different
18 regions. Trial-by-trial feedback would help us to clarify the role of ACC in the recognition of
19 conflict between outcome and reward (reward in this case would be correct prediction).

20 To our knowledge, this is the first study to identify activity in brain regions comprising a
21 cortico-subcortical network, over-and-above putative attentional and MNS systems, that may
22 underpin perceptual-cognitive superiority in sport anticipation tasks. Consistent with our
23 predictions, high-skill anticipators were more attuned to both early kinematic information and

1 deceptive movements than were their less-skilled counterparts; neuroimaging data also showed
2 greater activation of MNS and related structures in this group. The advantage was most profound
3 when viewing deceptive footage, but this was irrespective of occlusion – contrary to our
4 predictions. There was also neuroimaging evidence for changes in high-skilled participants’
5 allocation of attention when visual information was constrained, whether these shifts were
6 stimulus- or goal-driven. Although Yarrow et al.’s (2009) affordance competition model has
7 provided a suitable foundation for the predictions made, some activations – most notably those in
8 basal ganglia and cerebellum – have been conspicuously lacking in previous studies (e.g.,
9 Wright, et al., 2010; Wright, et al., 2011). However, there was robust evidence for greater
10 activation of these structures in the present data. Additionally, there was evidence for thalamic
11 activation in high-skill participants when viewing early-occluded footage; and evidence of
12 conflict monitoring (ACC) when viewing opponents’ deceptive actions. Hence, we tentatively
13 propose that these two highly interconnected structures (see Heyder, et al., 2004) may be added
14 to the affordance competition model, which would then more comprehensively illustrate the
15 interactions of diverse cortical and subcortical neural systems that characterize superior
16 anticipation skill in sport.

17 **End notes**

- 18 1. This sample size was recruited according to (a) power calculations based on preliminary
19 analysis of the response data and (b) threshold sample sizes previously established as
20 appropriate for such fMRI designs (Desmond & Glover, 2002; Zandbelt, et al., 2008).
- 21 2. The main effect of anticipation skill is not meaningful per se, because the groups were
22 formed on this basis. However, these data are presented in Table 1 to confirm the reliability
23 of the classification used; additionally, Figure 1 elucidates the extent to which overall

- 1 performance was moderated by level of occlusion and deception (i.e., whether high-skill
2 anticipators were superior uniformly, or only under specific conditions).
- 3 3. There were a large number of highly significant activations across all contrasts, even with
4 stringent corrections applied to p values. Therefore, to aid interpretability and
5 informativeness, activations were only included for group contrasts when they (a) satisfied
6 the imposed threshold criteria (FWE) and (b) related to the performance differences.
7

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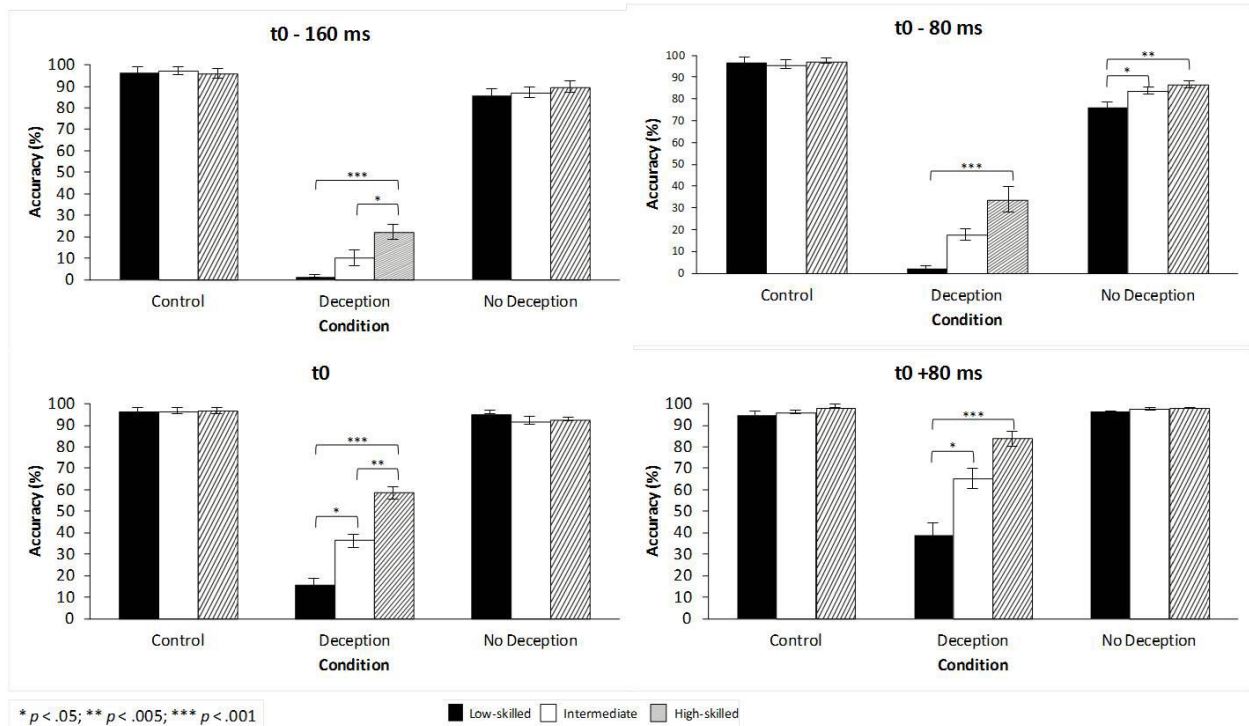
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Figure Captions

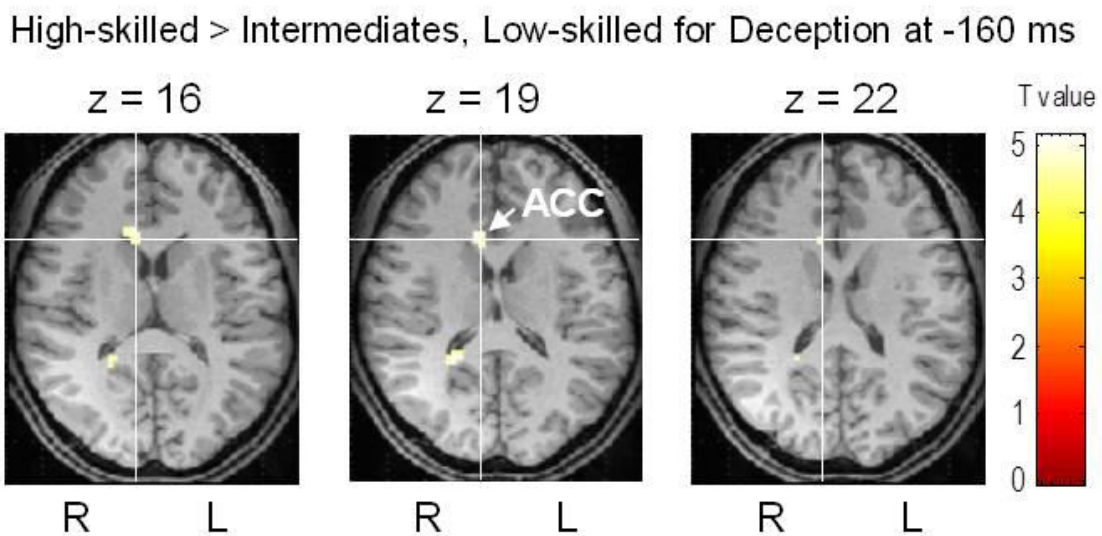
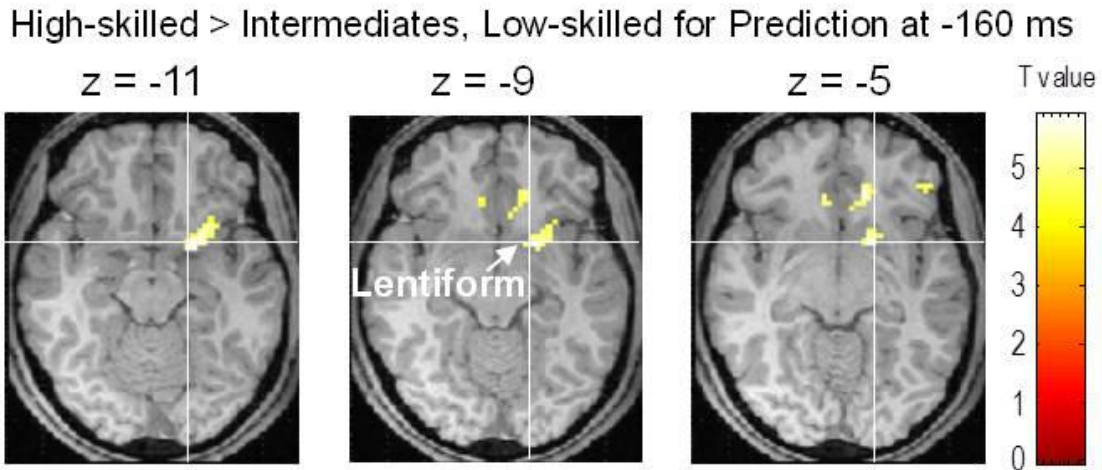
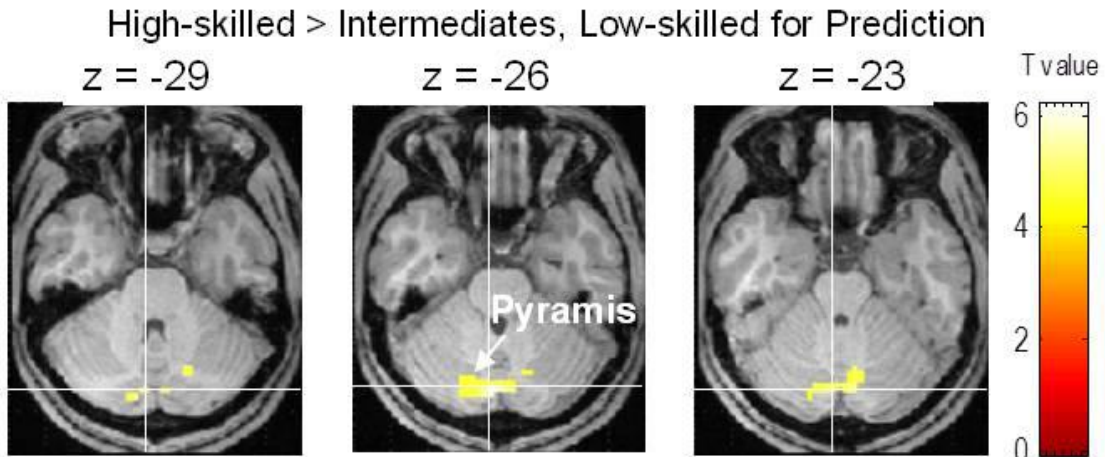
2 **Figure 1.** Main Simple Effects of Group, by Occlusion and Condition.



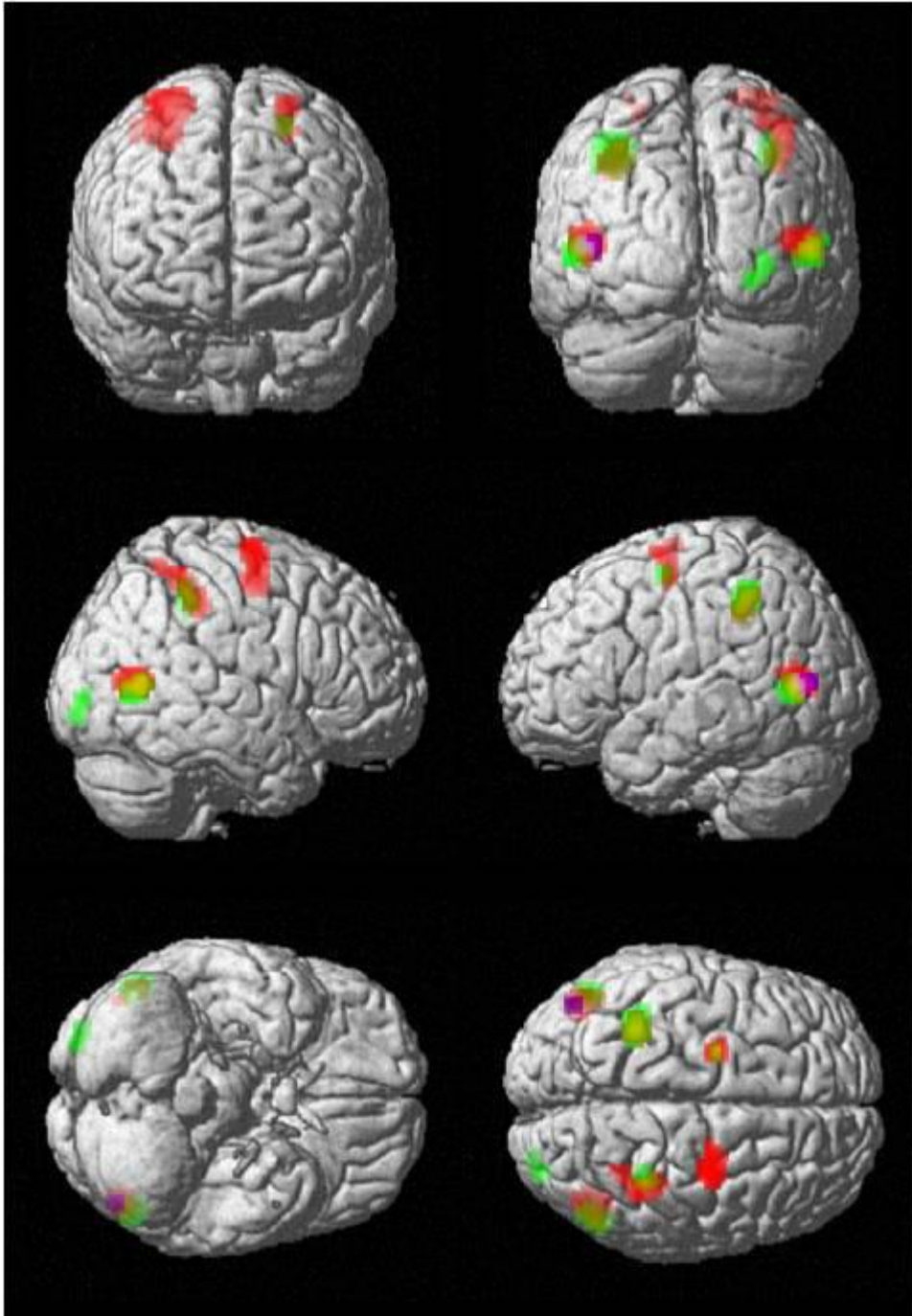
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- 1 **Figure 2.** Greater Cerebellar, Basal Ganglia, and Right Anterior Cingulate Cortex Activation for
- 2 Experts when Predicting Opponents' Movements.



- 1 **Figure 3.** Mirror Neuron System Activations for all Participants (red = high-skill; green =
- 2 intermediate; blue = low-skill).



3

4

1 Table 1

2 *Univariate F Tests and Pairwise Comparisons for all Main Effects*

Factor	Skill Level	DV	<i>M</i>	<i>SD</i>	
Group	Low	Prediction Accuracy	66.3	39.8	
	Intermediate		(%)*	72.7	32.8
	High			79.5	26.6
	Low	Response Time	2156.4	187.7	
	Intermediate		(ms)**	2175.9	199.7
	High			2063.8	210.9

* $F(2,35) = 38.43, p < .001, \eta_p^2 = .69$; High > Intermediate > Low, $p < .001$.^a

** $F(2,35) = 1.05, p > .05, \eta_p^2 = .06$.

Occlusion	-160 ms	Prediction Accuracy	65.3	46.4	
	-80 ms		(%)*	65.8	41.6
	t0			76.2	32.1
	+80 ms		86.3	18.3	
	-160 ms	Response Time	2199.5	157.0	
	-80 ms		(ms)**	2153.6	183.6
	t0			2095.7	221.4
	+80 ms			2069.1	259.0

* $F(3,105) = 111.16, \eta_p^2 = .76, p < .001$; +80 ms > t0 > -80 ms, -160 ms, $p < .001$.^b

** $F(3,105) = 4.84, \eta_p^2 = .12, p < .005; -160 \text{ ms} > -80 \text{ ms} > t_0, p < .05.$ ^a

Condition	Control	Prediction Accuracy	96.4	0.2
	Deception	(%)*	33.5	23.9
	No Deception		90.2	6.5
	Control	Response Time	1895.9	105.3
	Deception	(ms)**	2270.9	12.9
	No Deception		2221.6	67.7

* $F(2,70) = 947.49, \eta_p^2 = .96, p < .001; \text{Control} > \text{No Deception} > \text{Deception}, p < .001.$ ^b

** $F(2,70) = 40.47, \eta_p^2 = .54, p < .001; \text{Deception} > \text{No Deception} > \text{Control}, p < .001.$ ^b

1 ^a Tukey's HSD.

2 ^b Bonferroni-corrected for multiple comparisons.

- 1 Table 2
- 2 *Loci of Activation for Experimental Contrasts, Determined at a Familywise Error (FWE)-*
- 3 *Corrected Display Threshold $p < .05$ and Extent Threshold $k > 20$*

Region	BA	Size (voxels)	$p(\text{FWE})$	Z	x	y	z
<i>[a] High-skill > Intermediate, Low-skill for Prediction (Deception + No Deception), all Occlusion levels</i>							
R Pyramis	–	525	.001	6.05	6	-79	-26
R Culmen	–	525	.001	5.37	30	-40	-35
R IOG	18	192	.001	5.44	39	-85	-2
R STG	39	192	.026	4.56	60	-61	22
R SPL	19	62	.049	4.4	33	-76	49
<i>[b] High-skill > Intermediate, Low-skill for Prediction at -160 ms</i>							
L Lentiform Nucleus	–	49	.009	5.79	-18	5	-8
L SFG	6	22	.018	5.58	-9	32	61
L SEF	6	29	.001	5.26	-6	-7	58
L Cingulate Gyrus	24	29	.02	4.63	-15	2	46
R Thalamus	–	25	.002	5.12	3	-10	1
<i>[c] High-skill > Intermediate, Low-skill for Deception at -160 ms</i>							

R ACC	33	22	.003	5.06	9	17	19
<i>[d] -160 ms > -80 ms for Prediction, High-skill participants</i>							
L STG	22	340	0.003	5.07	-60	-16	1
R Precuneus	7	240	0.01	4.78	18	-55	70
L IPL	7	160	0.013	4.73	-45	-64	52
L IPL	39	160	0.015	4.69	-51	-61	46
R SFG	6	95	0.022	4.6	24	2	70

- 1 *Note.* In Montreal Neurological Institute coordinates. ACC = Anterior Cingulate Cortex; BA =
2 Brodmann Area; IOG = Inferior Occipital Gyrus; IPL = Inferior Parietal Lobule; MFG = Middle
3 Frontal Gyrus; SEF = Supplementary Eye Field; SPL = Superior Parietal Lobule; STG =
4 Superior Temporal Gyrus.

1 Table 3

2 *Loci of Activation for Prediction > Control; Determined at a Trend-Level Display Threshold $p <$*

3 *.005 and Extent Threshold $k > 60$*

Region	BA	Size (voxels)	Z	x	y	z
<i>All participants</i>						
L SEF	6	520	3.00	-24	-4	67
R SEF	6	376	3.16	21	-10	67
R SPL	7	210	3.92	36	-46	58
L MFG	6	148	4.06	-24	-7	61
L premotor	6	148	2.79	-39	-1	61
L premotor	6	148	2.88	-51	2	43
R IOG	18	136	3.42	24	-94	-8
L IFG	9	77	3.11	-45	8	25
L SFG	6	72	3.14	-3	17	49

4 *Note.* In Montreal Neurological Institute coordinates. BA = Brodmann Area; IFG = Inferior

5 Frontal Gyrus; IOG = Inferior Occipital Gyrus; MFG = Middle Frontal Gyrus; SEF –

6 Supplementary Eye Field; SFG = Superior Frontal Gyrus; SPL = Superior Parietal Lobule; STG

7 = Superior Temporal Gyrus.